Universidade de Aveiro Departamento de Biologia
2017

JOANA CRISTINA CARDOSO TEIXEIRA RIBEIRO

COMUNIDADES DE ANUROS TROPICAIS EM PAISAGENS AGRÍCOLAS: UMA ABORDAGEM INTEGRADA.

NEOTROPICAL ANURAN COMMUNITIES FROM AGRICULTURAL LANDSCAPES: AN INTEGRATED APPROACH.

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia e Ecologia das Alterações Globais (Especialização em Ecologia e Biologia Tropical), realizada sob a orientação científica do Doutor Amadeu M.V.M. Soares, Professor Catedrático do Departamento de Biologia da Universidade de Aveiro, e co-orientação do Doutor Guarino R. Colli, Professor Associado do Departamento de Zoologia da Universidade de Brasília.

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Dedico este trabalho à minha família, especialmente aos meus avós, que mesmo sem perceber muito bem o que a neta fazia, sempre me apoiaram incondicionalmente.

"Oh meu velho e indivisível, Avôhai…"
Zé Ramalho, Avôhai

"So may the sunrise bring hope;
Where it once was forgotten;
Sons are like birds;
Flying upward over the mountain."
Iron & Wine, Upward Over the Mountain

o júri

presidente

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agradecimentos

Os últimos quatro anos foram, sem dúvida, os mais desafiantes que já vivi. No entanto, não vivi esta aventura sozinha. Na verdade, só consegui finalizar este projecto porque pude contar com a ajuda, o companheirismo e a boa-vontade de muita gente, alguns dos quais passarei a nomear a seguir. Começando pelo início da história, tenho de agradecer em primeiro lugar à pessoa que me deu esta oportunidade, o Professor Amadeu Soares, que se viria a tornar meu orientador, acompanhando e amparando-me durante estes loucos 4 anos. Gostaria igualmente de agradecer ao meu co-orientador, o Professor Guarino Colli que, depois de tantas dificuldades foi um dos poucos que permaneceu ao meu lado neste projecto.

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agradecimentos (continuação)

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palavras-chave

Anfíbios, agricultura, características biológicas, diversidade funcional, diversidade filogenética.

resumo

Atividades antrópicas como a agricultura e a pecuária são as principais causas da perda de biodiversidade. A expansão agrícola é especialmente nociva nos trópicos, onde o investimento agrícola responde a importantes demandas sociais e económicas, e a biodiversidade é especialmente alta e única. O arroz é a cultura alimentar mais importante do mundo. Dada a sua natureza, localização e extensão a nível global, os campos de arroz irrigado são invariavelmente utilizado pela fauna nativas. Determinar como as comunidades que vivem nesses agroecossistemas são afectadas é, portanto, de extrema importância. O Cerrado, a maior e mais diversa savana do planeta, encontra-se sob extrema pressão antropogénica, com 50% do bioma atualmente sob uso humano direto. Os anfíbios estão entre os vertebrados mais ameaçados do planeta, desempenhando papéis de destaque no funcionamento dos ecossistemas. Como o seu ciclo de vida é particularmente complexo, investigar a forma como as populações de anfíbios são afectadas por atividades antropogénicas requer uma abordagem integrada e multidimensional, a várias escalas. Com este projecto pretendeu-se avaliar a forma como a comunidade de anuros do Cerrado está a ser afetada pela pressão agrícola, avaliando o risco de extinção, analisando os traits selecionados, e a variação na diversidade taxonómica, filogenética e funcional em diferentes escalas, bem como a conectividade funcional dos anuros em culturas de arroz. Determinou-se que o risco de extinção de risco oficial dos anfíbios do Cerrado se encontra subestimado. O local de reprodução, habitat e tamanho da postura são preditores de elevado risco de extinção em anuros. O sudoeste e região central do bioma são as principais regiões de espécies de alto risco de extinção, e devem ser priorizados para a conservação. Concluiu-se também que a conversão do habitat e a gestão agrícola causaram profundas alterações na comunidade de anuros, com o aumento da divergência funcional e dramática perda de diversidade funcional e filogenética em ambientes agrícolas. Anuros com distribuição restrita, especialização de habitat, posturas pequenas e grande tamanho corporal foram excluídos dos ambientes agrícolas. Adicionalmente, anuros provenientes de culturas apresentaram menor condição corporal. Assim, a conversão de vegetação natural em plantações de arroz irrigado resulta na extinção local de muitas espécies, independentemente da sua especialização, e no decréscimo dos índices de condição corporal nas espécies mais resistentes. A presença de abundantes fragmentos florestais e de corpos de água é determinante para a manutenção de níveis elevados de diversidade funcional e filogenética, e ainda para assegurar a conectividade funcional para as populações de anuros em paisagens agrícolas.

keywords Amphibians, agriculture, functional diversity, phylogenetic diversity, traits.

abstract Anthropogenic activities such as agriculture and cattle farming are the main causes of biodiversity loss. Agricultural expansion is especially detrimental in the tropics, where agricultural investment meets important social and economic demands, and biodiversity is especially high and unique. Rice is the world's most important food crop. Given its nature, location and extension worldwide, irrigated rice fields are invariably used by the native fauna. Determining how communities living in these agroecosystems are shaped is therefore of the utmost concern. The Cerrado, the world's largest and most diverse savanna is experiencing extreme anthropogenic pressure, with 50% of the biome currently under direct human use.Amphibians are among the world's most threatened vertebrates, playing keystone roles in ecosystem functioning. Given the inherent complexity of their life cycle, approaching how amphibian populations are affected by anthropogenic activities requires an integrated, multidimensional approach, at multiple scales. This project sought to assess how the anuran community of the Cerrado is being affected by agricultural pressure, assessing the extinction risk, analyzing the selected traits, and variation in taxonomic, phylogenetic and functional diversity at different scales, as well as the functional connectivity of frogs in rice crops. The official extinction risk is underestimated for the anurans of the Cerrado. Breeding site, habitat specialization, and clutch size are predictors of increased extinction risk. The southwest and central regions of the biome are the main hotspots of increased extinction risk, and should be prioritized for conservation. Habitat conversion and crop management caused profound changes to the anuran community, causing increased functional divergence and dramatic loss of functional and phylogenetic diversity in agricultural environments. Anurans with restricted range, habitat specialization, small clutches and large body size were excluded from agricultural environments. Additionally, frogs from agricultural environments had lower body condition. Thus, the conversion of natural vegetation to rice crops results in such environmental stress, that large subsets of species are driven to local extinction irrespective of their specialization, and even the more resilient species exhibit lower body condition. The presence of abundant forest fragments and water bodies is crucial for the maintenance of high levels of functional and phylogenetic diversity, and also to ensure functional connectivity for anuran populations in agricultural landscapes.

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Rien dans la vie est à craindre,
ce est seulement pour être entendu.
Ce est maintenant le temps de mieux comprendre,
de sorte que nous pouvons craindre moins.
Marie Curie

Chapter 1

General Introduction

1. INTRODUCTION

1.1. Worldwide biodiversity crisis

Biodiversity is currently facing a worldwide decline under increasing anthropogenic pressure (Barnosky et al., 2011). According to Ceballos et al., (2015) the average rate of vertebrate species loss over the last century is up to 100 times higher than the background rate, revealing an impending sixth mass extinction.

Biodiversity loss, caused by disturbances such as species overexploitation, habitat loss, climate change, or invasive species (Brook et al., 2008; Dunn et al., 2009), compromises the sustainability of ecological processes and the provision of ecosystem services (Cardinale et al., 2012).

Agriculture represents the largest landuse, occupiyng ca. 38 % of the world's terrestrial surface (Foley et al., 2011). The impacts agriculture has on biodiversity are varied and complex, occurring at both habitat and landscape level (Weyland et al., 2012)

Global pressure to further increase food production in coming decades will be enormous, as the world population is projected to approach 11 billion by the end of this century, with the population of Africa nearly quadrupling (United Nations, 2013). In fact, the global extent of cropland is currently expanding faster than at any time in the past 50 years (Grassini et al., 2008). Future expansion of agriculture will be especially detrimental for tropical ecosystems (Dobrovolski et al., 2011; Laurance et al., 2014). The greatest agricultural expansion will occur in South America and Sub-Saharan Africa (Bruinsma, 2009; World Bank, 2009), which have large areas with unexplored agricultural potential. These include rainforests, such as the Amazon and Congo Basins, as well as vast semi-arid biomes, such as the Cerrado South America or the Miombo and Guinea savanna-woodlands of Africa. Beyond feeding the growing populace and eliminating hunger, rising incomes in many developing nations will result in increased demand for meat and dairy products, bioenergy production and bio-feedstocks for industry (Fargione et al., 2012; Scharlemann and Laurance, 2008). These needs will inevitably be met by expanding agricultural systems stressed by climate change (Nelson et al., 2009).

Tropical ecosystems sustain much of the Earth's biological diversity (Myers et al., 2000), provide countless natural products and services to human communities (Grimes et al., 1994) and play key roles in the global carbon and hydrological cycles (Avissar and Werth, 2005; Fearnside, 2000). Unfortunately, many tropical ecosystems are being disrupted by large-scale land-use change and other environmental alterations (Laurance et al., 2014), facilitated by by improved crop and soil management practices that support higher yields. Furthermore, road construction and improving medical technologies are allowing humans to colonize areas once plagued by diseases (Hotez et al., 2009).

Expanding agriculture could be particularly detrimental for biodiversity hotspots, terrestrial biogeographic regions that sustain exceptional species richness and endemism and have suffered severe loss of their original vegetation (Mittermeier et al., 2004; Myers et al., 2000). Tropical and subtropical ecosystems predominate in over half of the hotspots (Mittermeier et al., 2004). In addition to their many known species, hotspots are believed to contain most of the Earth's undescribed species, many predicted to be restricted endemics (Joppa et al., 2011; Scheffers et al., 2012) and unlikely to survive in disturbed environments (Giam et al., 2012). Unfortunatelly, hotspots have highly dense and rapidly growing human populations (Cincotta et al., 2000), often struck by extreme poverty (Fisher and Christopher, 2007) and with low development scores (Jha and Bawa, 2006). Hotspot countries with the highest population growth rates and lowest human development had the greatest deforestation rates (Jha and Bawa, 2006). Demands to increase food production, promote economic growth, and exploit natural resources could inflict high environmental costs on hotspot nations.

Many tropical landscapes are nowadays composed of crops, plantations, and secondary, logged, and fragmented forests. Relative to intact forest, biodiversity is reduced in all modified tropical forests (Gibson et al., 2011), although to the smallest degree in selectively logged forests (Edwards et al., 2011; Putz et al., 2012). Biodiversity can be moderate in some mixed-cropping and agroforestry systems (Perfecto and Vandermeer, 2010), but is typically much reduced in plantation monocultures (Barlow et al., 2007; Fitzherbert et al., 2008; Ziegler et al., 2009). Mosaics of disturbed and secondary habitats can provide important habitat and foraging sites for forest species, as well as stepping stones and corridors for biotic dispersal and animal migration (Barlow et al., 2007; Chazdon et al., 2009; Pereira

and Daily, 2006; Perfecto and Vandermeer, 2010). Such mosaics can also be managed in some cases to benefit agriculture by promoting natural ecosystem services such as pest control and pollination (Boreux et al., 2013). The natural values of intensively managed farmlands and pastures are typically much lower than those of structurally more complex environments, such as logged and secondary forests, mixed plantings, and well-managed agroforestry systems (Edwards et al., 2011; Perfecto and Vandermeer, 2010).

Given the massive anthropogenic pressure on tropical biomes, protected areas are the core of conservation efforts in these regions. Approximately 6.6% of all tropical and subtropical forests are now in strictly protected areas (Jenkins and Joppa, 2009). However, protection of drier tropical habitats, including grasslands, savannas, and shrublands, is lower, with 5.9% in strictly protected areas and 12.5% in all reserve categories (Jenkins and Joppa, 2009). Although the network of tropical protected-areas has dramatically improved in the last 25 years, it is still inadequate because many threatened and locally endemic species fall entirely outside of protected areas (Rodrigues et al., 2004). In addition, many reserves are imperiled by illegal encroachment, logging, hunting (Curran et al., 2004; DeFries et al., 2005; Harrison, 2011; Laurance et al., 2012). Reserves are thus becoming geographicly isolated and, as their surrounding habitats become increasingly modified, reserves and their biodiversity will become increasingly imperiled.

Understanding the factors behind biodiversity loss is among the main issues in ecology, and absolutely pivotal for decelerating the current species extinction rate. However, the complexity and importance of this issue has not been met by the metrics used, e.g. species richness. An important component of biodiversity loss that succedes or even precedes species extinctions is the elimination of ecological interactions in which those species are engaged (Aizen et al., 2012; Tylianakis et al., 2008). As many key functional aspects of ecosystems depend on biotic interactions, their loss may have pervasive effects, accelerating species local extinction, impairing ecosystem functions, and ultimately collapsing the derived services provided to humans (Díaz et al., 2013).

The collapse of biological interactions and their associated ecological functions may frequently precede the complete disappearance of species, i.e., when a species' abundance is so reduced as to represent its functional extinction (Säterberg et al., 2013; Wilkie et al., 2011).

Biotic interactions are thus a major but often neglected component of biodiversity that needs to be considered in order to assess the 'health' of ecosystems and define critical indicators providing early diagnosis of environmental problems (Aizen et al., 2012; Dirzo et al., 2014; Tylianakis et al., 2008).

However pessimistic most predictions may appear, recent estimates of extinction risk from a wide range of ecosystems indicate that real empirical data often exceed predicted extinctions (Maclean and Wilson, 2011). Hence, we are still far from having adequate tools to predict species loss attributable to major anthropogenic disturbances such as habitat loss (He and Hubbell, 2011). In a research field still dominated by species richness as the diversity metric (Cardinale et al., 2012), adequate assessment of biodiversity loss and consequent effects on ecosystem functions and services may be impaired, ultimately compromising the effectiveness of every resultant management and conservation plan. Thus, there is an urgent need to quantify and predict the effects of disturbance on biodiversity patterns to guide conservation efforts and the management of ecological resources.

1.2. The value of ecophysiological traits in ecology

Analyses of past and projected extinctions have revealed highly non-random patterns in extinction risk (Anderson et al., 2011; Murray et al., 2011b; Olden et al., 2007; Thuiller et al., 2011; Tingley et al., 2013). Thus, not all species are equally at risk of extinction. A species' vulnerability to extinction depends on extrinsic threats such as habitat loss or invasive species, and on its intrinsic ability to respond to such threats (Cardillo et al., 2005; Collen et al., 2011; Murray et al., 2014). A species' response to threats is largely mediated by its traits, specific characteristics, related to physiological, morphological, and life-history features inherent to the organism and measurable at the individual level (Violle et al., 2007).

According to the habitat template theory of Southwood, (1977), the habitat provides the template on which evolution shapes characteristic life-history strategies through natural selection. Consequently, major environmental drivers influence the fitness of the species in a consistent manner, depending on the traits they possess, resulting in species sorting (McGill et al., 2006; Southwood, 1977; Webb et al., 2010). The interaction between traits and

environmental conditions is known as environmental filtering (e.g., Webb et al., 2010) a concept describing how traits are filtered in the regional species pool to yield the final trait composition, species composition and relative abundance in the community (Fig. 1.1). However, natural selection and species sorting do not operate at the level of single traits, but on whole organisms carrying multiple traits. Consequently, species performance will be a function of combinations of traits that synergistically present an adaptive response to the environment (Verberk et al., 2013, 2008).

Given the determinant role traits have on community composition, the ability to predict which species are more prone to go extinct - a major goal of conservation biology - can be achieved through trait-based approaches. While classic taxon-based approaches compare species assemblages (e.g., taxonomic composition, species richness, abundance measures) and relate them to differences in environmental conditions (Hawkins et al., 2010; Lancaster et al., 2009), trait-based approaches focus on the species' attributes that determine its ability to deal with environmental changes. Compared to taxon-based, trait-based approaches have i) improved mechanistic understanding of species–environment relationships (Kearney and Porter, 2009) and, consequently, ii) greater generality of such relationships because of applicability across regions.

The use of species traits in ecology is rapidly expanding (Doledec and Statzner, 2010; Menezes et al., 2010; Vandewalle et al., 2010), showing great potential for transforming descriptive field studies into a predictive science of community ecology. However, trait-based approaches are yet to deliver on this promise.

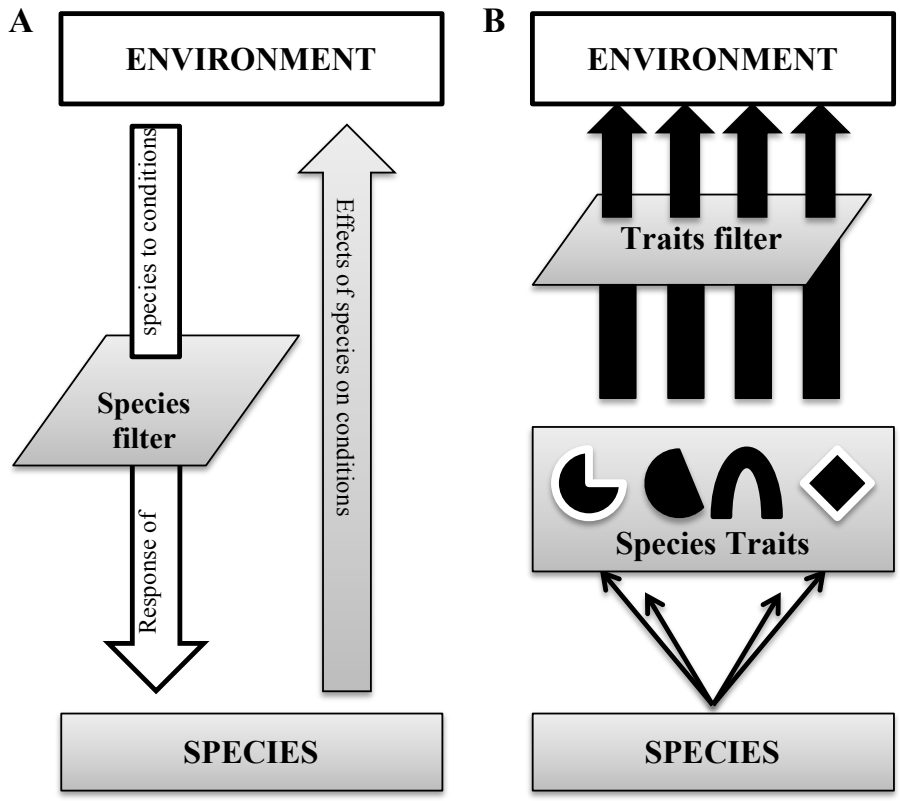

Figure 1.1 Schematic representation of the taxon-based (A) and trait-based (B) approaches to understanding the differences in species assemblages resulting from abiotic and biotic conditions. Trait-based approaches are based on the notion that the habitat acts as a templet that mechanistically explains how major environmental drivers influence the fitness of the species, depending on the combination of traits they possess.

1.2.1. Predicting extinction risk

The IUCN Red List is arguably the most useful list of species extinction risk and has been used to raise awareness about threatened species, guide conservation efforts and funding and set priorities for protection (Baillie et al., 2008; Mace et al., 2008; Martín-López et al., 2011; Rodrigues et al., 2006). The Red List classifies species into different risk categories according to a set of quantitative criteria assumed to translate extinction risk, such as population range, population size, decline and/or spatial fragmentation (IUCN, 2001). Species

are classified as Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) or, if threat criteria are not met, as Least Concern (LC). If available data are insuficient to determine conservation status, species are categorized as Data Deficient (DD). Hence, a species categorized as threatened can have stable populations and be listed because of other factors assumed to raise the extinction risk, such as a limited number of subpopulations.

Despite the unquestionable value of this system for conservation, there is an increasing awareness that many extinctions go unnoticed because they occur within small, strongly neglected organisms (e.g., Cardoso et al., 2010; Dunn et al., 2009; Régnier et al., 2009; Triantis et al., 2010). Worldwide conservation efforts have mostly relied on a few emblematic groups, because monitoring populations of rare, inconspicuous or unpopular species living in unaccesible or largely unsampled areas is a challenging process and would hardly be funded. Although Red List criteria are meant to be applicable to the majority of described species, several logistic constraints and intrinsic human preferences have produced a deep bias (Domínguez Lozano et al., 2007). While almost all of the mammalian and avian species have been evaluated, *ca*. 24% of amphibians remain DD and only 0.5% of the described arthropod species worldwide have been evaluated (IUCN, 2015). This portraits the Red List as heavily biased towards large species with wide distribution ranges and high dispersal abilities (i.e., those that are easily sampled), disregarding small species with narrow distribution ranges and low dispersal abilities, which constitute the vast majority of the planet's biota, particularly local endemics. Hence, the most threatened species may be systematically excluded.

The Red List criteria are difficult to apply using the information available for many species (Kozlowski, 2008) because of four main shortfalls (Cardoso et al., 2011): (1) many species are undescribed (the Linnean shortfall); (2) the distributions of described species are largely unknown (the Wallacean shortfall); (3) species' abundances and their changes in space and time are unknown (the Prestonian shortfall); and (4) species' ecology and sensitivity to habitat changes are largely unknown (the Hutchinsonian shortfall). These four shortfalls stem from the fact that basic taxonomy and natural history research is scarce and underfunded. Poor basic knowledge impairs reliable extinction risk attribution. However, even if the required information could be gathered, the current criteria may not be appropriate for many species. Thus, further frameworks should be used complementary to the Red List in order to

thorouhgly assess extinction risk and guide conservation practice.

Some life-history traits are related to colonization ability and extinction risk, which means that traits may be used as surrogates for extinction risk when population data are scarce (Fagan et al., 2001; Henle et al., 2004). Fagan et al., (2001) were able to predict the general extinction vulnerability of 60 out of 72 mammals simply by knowing body size, age at first reproduction, and average number of offspring. Worldwide, the extinction vulnerability of bat species was correlated with small geographic ranges and low wing aspect ratios (Jones et al., 2003). Declining amphibian species in Central America had large body sizes, restricted elevational ranges and aquatic habitats (Lips et al., 2003). Other factors, including clutch size, body size and ecological niche, have also been identified as potentially important (Hero et al., 2005; Lips et al., 2003; Stuart et al., 2004; Williams and Hero, 1998). In fact, small geographical range size has been consistently identified as the most important predisposing factor to decline (Cooper et al., 2008; Gaston and Fuller, 2009; Murray and Hose, 2005).

Despite particular traits predisposing species or groups of species to decline, external factors must be considered (Cardillo et al., 2008; Davies et al., 2006). The effects of a threat can be expected to vary spatially and across species because unique suites of traits respond differently to a disturbance (e.g. habitat specialists are particularly vulnerable to habitat destruction (Norris and Harper, 2004)). This results in complex, context-dependent and/or indirect pathways to decline (Blaustein and Kiesecker, 2002; Davidson et al., 2009). Murray et al., (2011a) for example, show that the spatial distribution of chytridiomycosis is a better correlate of decline than range size in Australian frogs, while Bielby et al., (2008) showed that the intrinsic traits of infected species correlate with whether they have suffered rapid declines or not as a result of infection. Given the diversity of known threats and the array of ecological and life-history traits that predispose species to decline, untangling the complex interactions that result in specific pathways to decline or extinction is a challenging task (Bielby et al., 2009, 2008; Blaustein and Kiesecker, 2002; Davidson et al., 2009) but one that is important for predicting further declines and, more importantly, improving our ability to do something about them (Wilson et al., 2007). For these reasons, it has been recently stressed that considering both intrinsic traits and extrinsic threats together is pivotal for thoroughly assessing extinction risk (Cardillo et al., 2008).

1.2.2. Community response to disturbances

Data on species composition only provides context and bioregion-specific information, and metrics such as richness or diversity do not translate ecological functions (Vandewalle et al. 2010). Furthermore, our limited knowledge of population dynamics, physiological tolerances, ecological constraints, or long-term and indirect effects can impair our ability to investigate ecological ramifications of biodiversity loss.

Ecophysiological and behavioral traits are consistent among populations of the same species, are easily access than demography data, and are associated with various environmental variables of interest (Cane et al., 2006; Devictor et al., 2008). For example, traits such as body size, determine the spatial scale at which the organisms perceive their environment and control access to resources of various kinds (mineral nutrients, prey items, nest sites, pollinators, e.g.,(Larsen et al., 2005; Petchey and Gaston, 2006a) affecting species turnover among habitats, along environmental gradients or between regions (Mason et al., 2007). Hence, incorporating widely-available information about species traits and looking for consistent responses within groups that share traits would allow predictions of general patterns that could be applied to a range of related taxa and provide a mechanistic link between disturbances and patterns of response within communities (Mouillot et al., 2013a; Williams et al., 2010).

This approach would also be fruitful for devising management plans when land managers and stakeholders face decisions associated with landscape or global changes and how these might impact communities or particular species of conservation concern. Furthermore, if the traits that determine species response to environmental change or disturbance are positively correlated to those that determine functional importance, then functional trait composition and overall ecosystem function may also change dramatically (Petchey and Gaston, 2006b). In fact, measures of the functional traits within a community have been shown to be better predictors of ecosystem processes than species diversity metrics (Flynn et al., 2011; Naeem et al., 2012; Thompson et al., 2015). Quantifying and predicting functional community structure within a context of increasing disturbance is thus required to

anticipate the potential loss of ecosystem services that is indisputably associated with biodiversity erosion (Cardinale et al., 2012).

Specifically, in anthropogenic habitats, assemblages may be filtered by species dispersal ability, with dispersal being one of the most important traits for assemblage recovery after disturbance in both vertebrates and plants (Kyle and Leishman, 2009; Moretti and Legg, 2009). However, disturbed ecosystems have also been found to select for smaller and more fecund species, while larger slow-growing species are better suited to stable habitats (Chiu and Kuo, 2012; Statzner and Bêche, 2010). Disturbance and eventual recovery also affect vegetation structure, microclimate, environmental stressors such as aridity, and resource spectra such as soil fauna or plant seeds, with implications for other functional traits (Entling et al., 2007; Schirmel and Buchholz, 2011). Therefore, trait responses to disturbance are complex and may be mediated by multiple environmental effects in addition to filters of dispersal ability.

In recent years, trait analyses have been used for evaluating ecosystem health, especially for certain organisms, such as macroinvertebrates, which have been viewed as a promising biomonitoring tool to assess human impacts on freshwater habitats (e.g. Doledec and Statzner, 2010; Culp et al., 2011).

1.2.3. Ecosystem services and resilience

The loss of biodiversity due to anthropogenic activity can have profound impacts on the functional properties of ecosystems and the services they provide (Naeem et al., 2012). Recent emphasis on ecosystem services for attributing value to ecosystems and promote their sustainable use (Millennium Ecosystem Assessment, 2005) has drawn attention to the ways in which different organisms contribute to the delivery of ecosystem services (Díaz et al., 2007; Luck et al., 2012; Suding et al., 2008). However, our ability to assess how ecosystem services are affected by anthropogenic activities is still incipient.

Disentangling how ecosystems provide multiple services consists first in allocating relevant ecosystem properties to each service, and identifying which organisms, or groups of organisms, control these properties (Kremen, 2005). Afterwards, it is necessary to discern the

key characteristics and mechanisms by which these organisms affect ecosystem properties (Hooper et al., 2005; Luck et al., 2012). Species functional traits influence ecosystem functioning directly by mediating changes in biotic controls (e.g., predation or competition) and indirectly through responses to changes in local environment (e.g., microclimates or disturbance regimes) (Chapin et al., 2000). This is being approached in an increasing number of studies, such as those identifying the functional roles of pollinators (Kremen et al., 2007), particular plant groups as nitrogen fixers (Spehn et al., 2002), soil or sediment engineers (Boyero et al., 2007) and different faunal groups (Heemsbergen et al., 2004). Such studies have identified functional traits as the key factors by which species (Díaz et al., 2007; Hooper et al., 2005; Luck et al., 2012) influence ecosystem properties, mostly structural plant traits (e.g. plant growth form, tissue chemistry, leaf morphology, canopy size and architecture), microbial ecophysiological traits and behavioural animal traits (feeding habit, substrate type, nesting activity, mobility, environmental and temporal niche). Hence, quantificatying the kind, range, and relative abundance of functional traits in biotic communities can greatly contribute to ecosystem service assessment and management (Díaz et al., 2007; Petchey and Gaston, 2006b).

Functional trait diversity, rather than the diversity of species per se, is the dimension of biodiversity most directly related to ecosystem functioning (Cadotte, 2013). Variation in functional trait diversity and composition due to land management can be a strong driver of ecosystem functioning and ecosystem services (Fig. 1.1).

Understanding the linkages between biodiversity and ecosystem services is especially crucial for predicting how changes in environment and management practices will impact the multiple ecosystem services provided by agroecosystems (Kremen and Miles, 2012; Power, 2010). Wood et al., (2015) state that a trait-based approach to agriculture that is analogous to that applied in broader ecology (e.g., Cadotte et al., 2011; de Bello et al., 2010; Violle et al., 2007) could help better identify the mechanisms underlying the role of agrobiodiversity in providing agroecosystem services. Biodiversity loss is known to affect not only ecosystem functioning but also crop yield (Daily, 1997). For example, landscape intensification may disrupt processes such as biological pest control (Perfecto and Vandermeer, 2010; Symondson

et al., 2002), crop pollination (Kremen et al., 2007; Ricketts et al., 2004) and resistance to plant invasion (Levine et al., 2004; Zavaleta and Hulvey, 2004).

As species differ in their potential contribution to ecosystem services, increasing biodiversity enhances the probability that a species that strongly enhances ecosystem functioning is present. Hence, the functional identity of one or few species dominating ecosystem processes becomes important. Sampling effects have been shown to be important in experiments with sown grasslands where the random inclusion of particularly productive species contributed to overall productivity (in addition to complementarity effects, Loreau and Hector, 2001). The chance of including a particularly effective species in a given environment appears to increase with the number of species in the available pool. Species redundancy means that a positive relation between diversity and functioning holds only for few species and additional species do not increase function, but plateau at higher diversity levels. However, redundancy is important because only high-diversity systems with redundancy in functional groups can be expected to provide the capacity for reorganization after disturbance. High diversity of functional groups may allow reorganizations after disturbances (Bengtsson et al., 2005), due to a high number of insurance species (the insurance hypothesis of biodiversity, Loreau et al., 2003). Surplus or redundant species may become even more important in an ever-changing environment, as formulated by the hypothesis of spatiotemporal insurance by biodiversity. In unpredictable human-dominated landscapes, diverse communities support species that may become important as soon as others disappear. Economically, this is an option value for the future. For example, Perfecto et al. (2004) found that high tree richness in coffee agroforestry supports a diverse bird community that turned out to increase predation on lepidopterans. Hence, these diverse coffee landscapes appeared to provide an important function with the prevention of potential pest outbreaks. The many solitary bee species on highland coffee are more effective pollinators than the few, but abundant, social species, thereby contributing to the positive relation of fruit set to bee diversity (Klein et al., 2003). This mechanism is similar to that of the collective role of rare plant species providing resistance to a grassland invader (Lyons and Schwartz, 2001). Removal of many rare plant species, but not removal of the same biomass of common species, enhanced invasion success of *Lolium multiflorum* (see also Levine et al., 2004). In such cases

many rare species may turn out to be more important for ecosystem functioning than few abundant species.

1.3. Functional & Phylogenetic diversity

Preventing dramatic and global loss of biodiversity, along with its consequences for ecosystem services is still possible through intensified and integrated conservation efforts. Thorough and effective magament and conservation plans are therefore urgent and can only be achieved if reliable ways to monitor biodiversity and accurately assess how land use intensification might affect ecosystem services have been developed (Mace and Baillie, 2007).

Classical biodiversity measurements such as species richness have relied on three main assumptions: (i) all species are equal (only relative abundances establish the relative importance of species), (ii) all individuals are equal (whatever their size) and (iii) species abundances have been correctly assessed with appropriate tools and in similar units (Magurran, 2004). However, species not only offer a wide range attributes, they are also likely to support many goods and services through ecosystem processes (e.g. Díaz et al., 2007). Hence, the first assumption of biodiversity measurement is not valid: some species carry more evolutionary history or functional traits essential to ecosystem processes than others (Cadotte and Davies, 2010; Mouillot et al., 2013b). This consensus has resulted in a growing focus on the diversity and values of functional traits that influence ecosystem functioning, as a tool for explaining the role of organisms in ecosystems and the ecological impacts of their loss (Petchey and Gaston, 2006b). Nonetheless, most studies addressing community assembly in human-modified landscapes rely on simplistic taxonomic metrics (Sodhi and Ehrlich, 2010) and leave important ecosystem-level

consequences unaddressed. Because the complex effects of environmental variation induced by human activities on species is ultimately mediated by specific characteristics (e.g. physiological constraints, habitat requirements, dispersal abilities), considering only taxonomic metrics may fail to provide accurate conclusions on the real consequences of anthropization on biodiversity. To attain more representative conclusions on the effects human activities have on communities, we must go beyond species number and account for different

components of biodiversity.

Functional (FD) and phylogenetic diversity (PD) are estimates of biodiversity based on ecological functions and evolutionary histories of species, respectively. FD describes the variability in ecological attributes among species and expresses ecosystem resistance, resilience and functioning (Petchey and Gaston, 2006a). Use of the term "functional diversity" has grown exponentially over the last decades (Petchey and Gaston, 2006a) and the concept of functional diversity is gaining a place of general importance in ecological research (Naeem, 2002). Measuring functional diversity is equivalent to measuring functional trait diversity, where functional traits are components of an organism's phenotype that influence ecosystem processes. There is an increasing body of literature demonstrating that functional diversity, rather than species diversity, enhances ecosystem functions such as productivity (Hooper and Dukes, 2004; Hooper et al., 2005; Petchey et al., 2004; Tilman et al., 1997), resilience to perturbations or invasion (Bellwood et al., 2004), and regulation in the flux of matter (Waldbusser et al., 2004). As functional diversity consists of the range and values of key morphological and physiological traits, communities with high numbers of species but low functional diversity can be said to have high functional redundancy (Petchey et al., 2007). This is because high functional redundancy occurs when species overlap in their traits, which may reflect niche overlap if traits are defined in a biologically appropriate way (Díaz and Cabido, 2001). Conversely, when each species present in a community represents a unique combination of traits, there is low functional redundancy. The most critical assumption in this formulation of functional redundancy is that the traits under consideration are those determining ecosystem functioning (Walker et al., 1999). High functional redundancy may result in limited loss of ecosystem functioning with species loss, while in communities with low functional redundancy, the loss of even a few species could have dramatic consequences for ecosystem functioning. According to Villéger et al., (2008), FD can be divided into three primary components – functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve). FRic represents the amount of functional space occupied by a species assemblage. FEve corresponds to how regularly species abundances are distributed in the functional space. Finally, FDiv defines how far high species abundances are from the center of the functional space. These facets are complementary and jointly describe the distribution of

species and their abundances within the functional space.

An important consideration for such a trait-based approach is to identify which functional traits and which species are relevant (Suding et al., 2008). Response traits are important because they indicate how species respond to environmental change, whereas effect traits are important because they indicate how species affect ecosystem processes (Lavorel and Garnier, 2002). Not all species are of equal importance for ecosystem processes; as dominant species make up the bulk of the community biomass, they will also be responsible for most of the ecosystem fluxes in energy and resources (Garnier et al., 2004).

PD measures the evolutionary differences among species based on times since divergence from a common ancestor (Faith, 1992), representing an estimate of phylogenetically conserved ecological and phenotypic differences among species (Cavender-Bares et al. 2009). This dimension may characterize the long-term evolutionary potential of specific clades to respond or adapt to current and future environments. Few studies have explored the influences of anthropic landscapes on FD or PD (Tscharntke et al., 2012), and most of which have focused on plant and invertebrate assemblages (e.g., Arroyo-Rodríguez et al. 2012; Aviron et al. 2005; Laliberte et al. 2010).

FD and PD were both advocated as two important facets of diversity respectively for ensuring the provision of goods and services (Díaz et al., 2007) and for representing an evolutionary history of conservation interest (Knapp et al., 2008; Mace et al., 2003). Metrics other than traditional diversity indices may thus be necessary to picture the actual trends. For example, a net increase in regional species richness may be accompanied by a decrease in functional diversity (Villéger et al., 2010), or two communities of equal TD may be composed of species with either highly similar or different phylogenetic histories (Forest et al., 2007). Similarly, any estimated measure of FD can also be decoupled from PD if some functional traits are under strong stabilizing selection or owing to competitive interactions within lineages (Prinzing et al., 2008). Taken together, the use of a multifaceted approach to describe the spatial distribution of biodiversity has recently proved to be useful for describing how biodiversity covaries in space, unravelling assembly mechanisms (Cadotte, 2013) and understanding the drivers explaining community composition (e.g. Bernard-Verdier et al., 2013; Graham et al., 2012; Huang et al., 2012; Pavoine et al., 2009). Measuring each of these

complementary biodiversity components is thus necessary for understanding the complete structure, composition and dynamics of natural communities (Maherali and Klironomos, 2007). Adopting an integrated view of biodiversity is also a great challenge for conservation planning.

Functional indicators can also greatly improve predicting the functions or services provided by an ecosystem as they are proxies for the rate, or relative importance, of particular processes (Vandewalle et al., 2010). If the traits that determine species response to environmental change or disturbance positively correlate with those that determine functional importance, then functional trait composition and overall ecosystem function may also change dramatically (Petchey and Gaston, 2006b). However, this concept is yet a neglected component in biodiversity monitoring programmes in most ecosystems (Feld et al., 2009).

1.4. The Cerrado

Brazil harbors outstanding biodiversity, sharing with Indonesia the top two positions of the world's "Megadiverse" countries (Mittermeier et al., 2000). However, not all Brazilian biomes have merited equal attention. While the Amazon and the Atlantic Forest have merited global recognition, the Cerrado has remained forgotten by scientists, environmentalists and general public, facing an increasingly threatening anthropic pressure.

The Cerrado is located in the center of Brazil, bordered by the Amazon forest to the north, the Atlantic forest to the south and southeast, and the *caatinga* to the northeast (Fig. 1.2). The 2nd largest biome of South America, this tropical savanna stretches for about 1, 500,000 km^2. Because of its wide latitudinal and altitudinal ranges, has great climatic and environmental diversity, encompassing considerable habitat heterogeneity. Ecological factors have acted in synergy to shape the native vegetation into several physiognomies. The typical vegetation consists of a mosaic of savanna, forest and grassland formations. The savanna formations are generally located on well-drained interfluves, whereas gallery forests follow the watercourses. As a consequence of this heterogeneity, the Cerrado presents high species richness and endemism of plants and vertebrates (Colli et al., 2002; Klink and Machado, 2005).

The Cerrado includes much of central Brazil and parts of northeastern Paraguay and

eastern Bolivia (Ab'Saber, 1977), occupiyng a central position in relation to other large South American biomes, with extensive borders with the two largest forest biomes (Amazonia and Atlantic Forest) as well as with the two largest dry regions (Caatinga and Chaco).

The Cerrado has a tropical wet and dry climate with intermediate rainfall between the wetter regions to the northwest and southeast and the drier areas to the northeast. Average annual rainfall varies between 125 and 200 cm and average annual temperature between 20° and 26° C (Ab'Saber 1977). The dry period lasts from 3 to 5 consecutive months (generally between May and September or October), during the winter of the Southern Hemisphere (Sarmiento 1983).

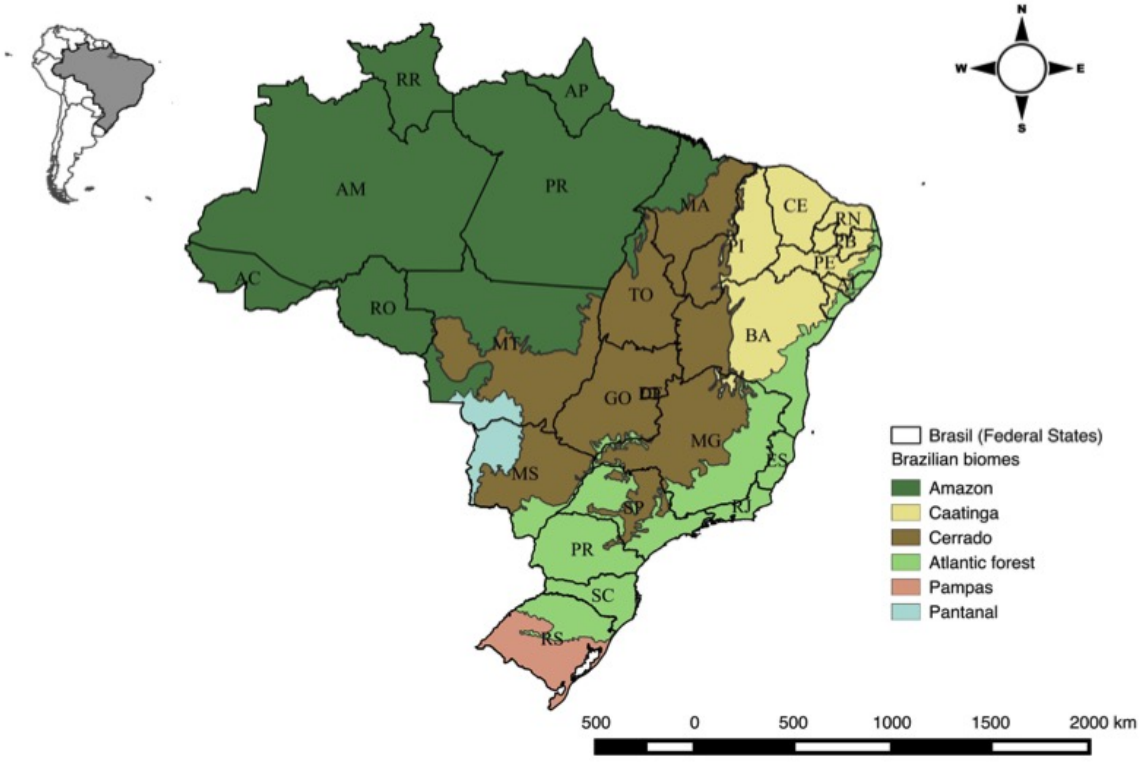

Figure 1.2. Geographical location of the Cerrado and Brazil's other 5 biomes. Federate units also represented: AC: Acre; AL: Alagoas; AM: Amazonas; AP: Amapá; BA: Bahia; CE: Ceará; DF: Distrito Federal; ES: Espírito Santo; GO: Goiás; MA: Maranhão; MT: Mato Grosso; MS: Mato Grosso do Sul; MG: Minas Gerais; PA: Pará; PB: Paraíba; PR: Paraná; PE: Pernambuco; PI: Piauí; RJ: Rio de Janeiro; RN: Rio Grande do Norte; RS: Rio Grande do Sul; RO: Rondônia; RR: Roraima; SC: Santa Catarina; SP: São Paulo; SE: Sergipe; TO: Tocantins.

Most of the Cerrado is on plateaus of crystalline or sedimentary blocks, whose continuity is broken by an extensive network of peripheral or interplateau depressions (Brasil and Alvarenga 1989). This geomorphological variation explains much of the distribution of plants in the Cerrado (Cole 1986). Savannas are the dominant phytophysiognomy, covering around 72% of the region, but patches of dry forests and complex belts composed of both dry forests and savannas give the region a mosaic-like aspect (Fig. 1.3) (Cardoso Da Silva and Bates, 2002). About 24% of the region represents this mosaic of savanna–forest transition, with a remaining 4% being dry forest. The tops of the plateaus are flat, gently rolling surfaces at elevations ranging from 500 to 1700 m. They are covered primarily by cerrado, a semideciduous to evergreen savanna-like vegetation growing on the deep, well-drained, and nutrient-poor soils (Eiten 1990). Five main structural types of cerrado are recognized by botanists (Eiten 1972): i) *cerradão,* a dense forest type (8–15 m tall) that often has a completely closed canopy; ii) *cerrado sensu stricto,* a woodland (5–8 m tall) with closed scrub and more scattered trees than in cerradão; iii) *campo cerrado,* an open scrubland (3–6 m tall) with few trees; iv) *campo sujo,* grassland (2–3 m tall) with scattered shrubs; v) *campo limpo,* grassland with few or no shrubs or taller woody plants.

Besides cerrado, other types of distinct savanna vegetation, called *campos rupestres*, and miscellaneous lithosolic campos occur on rocky outcrops. These habitats are limited to small patches on the plateaus and have a highly endemic flora (Eiten 1990). Narrow fringes of gallery forest often border small rivers and streams of the region. Gallery forests on the plateaus grow on narrow belts of soils rich in organic matter (Eiten 1990). They are evergreen, have trees that are on average 20–30 m tall, and possess a dense understory of low stature (Ribeiro and Walter, 2008). Commonly associated with gallery forests are stands of a species of palm, *Mauritia flexuosa,* locally known as *veredas.* The peripheral depressions are generally flat surfaces of little relief (100–500 m in elevation) that are ocasionally inter- rupted by the presence of steep-sided hills.

The percentage of species endemic to the Cerrado varies across different groups of organisms: vascular plants (44%), amphibians (30%), reptiles (20%), mammals (11.8%), and birds (1.4%) (Myers et al., 2000). However, because large areas of the Cerrado remain unexplored (Silva, 1995), these numbers will likely change when additional biological

inventories are conducted. At present, we still know little about how these endemic species are distributed across the Cerrado or how they evolved.

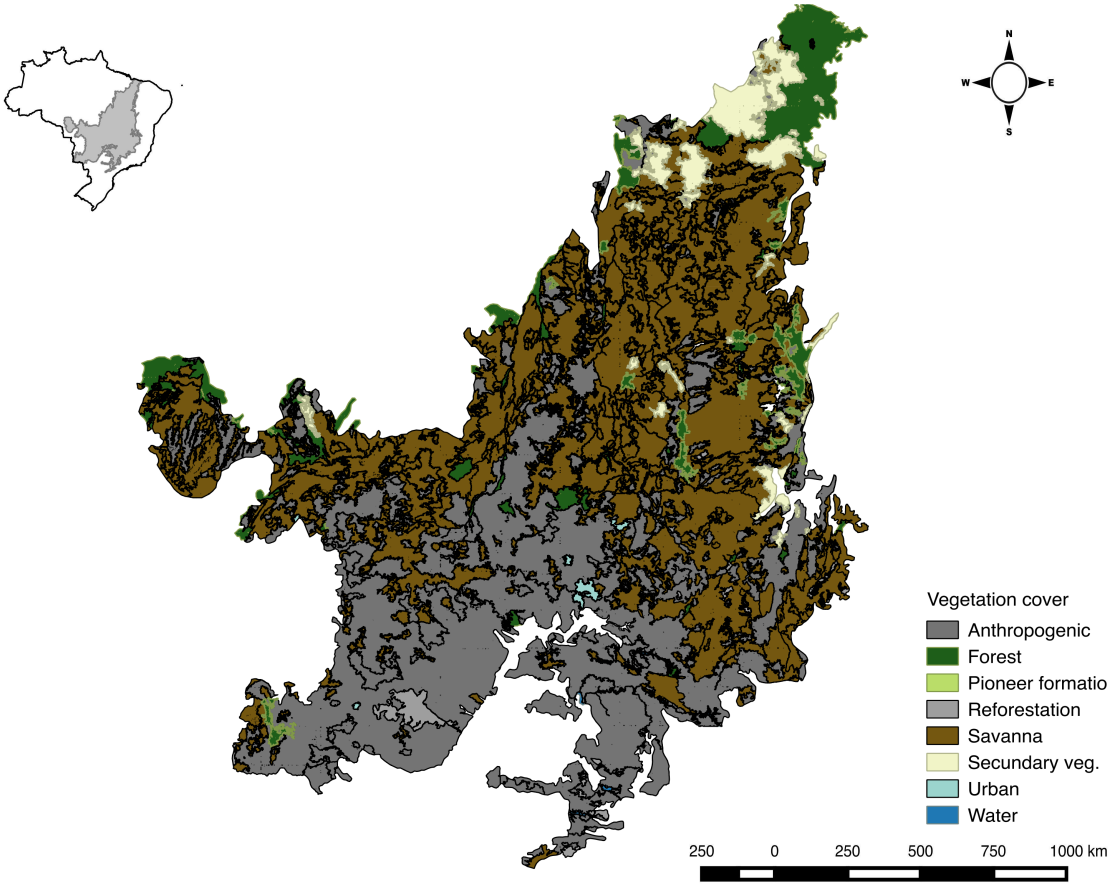

Figure 1.3. Geographic distributions of the main phytophisiognomies of the Cerrado. Anthropogenic land-use is also represented (MMA, 2007).

1.4.1. The anthropization of the Brazillian savana

Up to the mid-twentieth century, the Cerrado had no economic value and was unattractive due to the scrubby nature of the vegetation, apparent low faunal densities,

pronounced dry season and frequent fires. By the 1950's, the Brazilian government was determined to develop the "empty" center of the country, building the new capital city, Brasília, in the core of the Cerrado and stimulating agricultural development through subsidies, tax incentives, loans and guaranteed prices. These incentives, along with the development of appropriate technologies enabled farmers to deal with nutrient-poor and acidic soils, investing in large-scale fertilization, high yield/drought-resistant crop varieties and the heavy use of herbicides, pesticides and modern machinery. After all these agronomic investments, the Cerrado's wide grasslands and dry soil offered much less resistance to land clearing and mechanical mobilization than rainforests.

Over the past six decades the Cerrado became Brazil's largest source of soybeans and pastureland, a significant producer of rice, corn, and cotton (Klink et al., 1999). From a revenue generation perspective, the benefits of commercial agriculture in the Cerrado are clear as soy is one of the main brazilian export commodities and the Cerrado supports the largest cattle herd in the country (Klink et al., 1999). Consequently, much of the biome's landscape became a mosaic of "islands" of native vegetation surrounded by vast areas of homogeneous agricultural lands. Nearly 50% of the Cerrado is currently under direct human use, and about 35% of its total natural cover has been converted into planted pastures and crops (Allan, 2003).

The frantic conversion of the Cerrado into a massive agricultural land may be a side effect of the international pressure to halt deforestation in the Amazon. In the search for alternatives, the Cerrado has often been targeted (Ab'Saber et al. 1977). In fact, the Cerrado bovine herd as always been larger than the Amazon's and the percentage of area used for crops has been superior in the Cerrado since 2005 (Fig. 1.4). The Brazilian government's appreciation for the uniqueness of the Cerrado's biodiversity has developed slowly. The first major conservation initiative occurred in 1997, when the Brazilian Ministry of Environment promoted a workshop, with over 200 scientific experts on the region, to define priority areas for conservation in the biome. It followed the same methodology applied earlier for the Atlantic Forest and Amazonia (Cavalcanti 1999). Several criteria for assessing biodiversity value were used, such as number of endemic species, species richness, presence of rare or endangered species or both, and sites of unique communities or key areas for migratory

species. The group identified a total of 87 priority areas that formed the basis for seting the current protected areas in the biome (Fig. 1.5). The urgency for conservation action in a priority area was determined by cross-referencing biodiversity data with the human-pressure and land cover change data (Cavalcanti 1999).

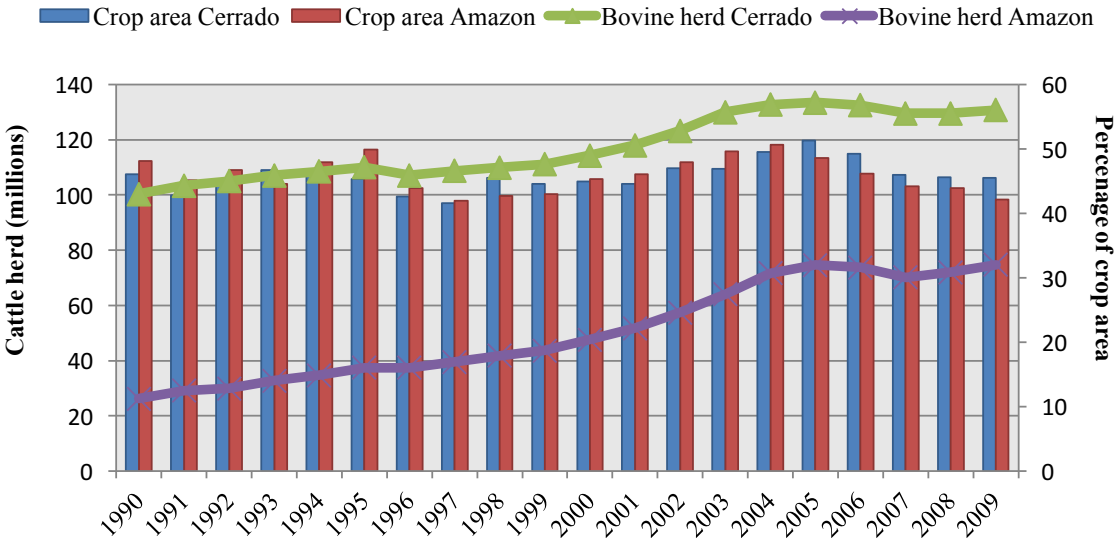

Figure 1.4. Percentage of crop area and size of cattle herd in the Cerrado and Amazon from 1990 to 2009.

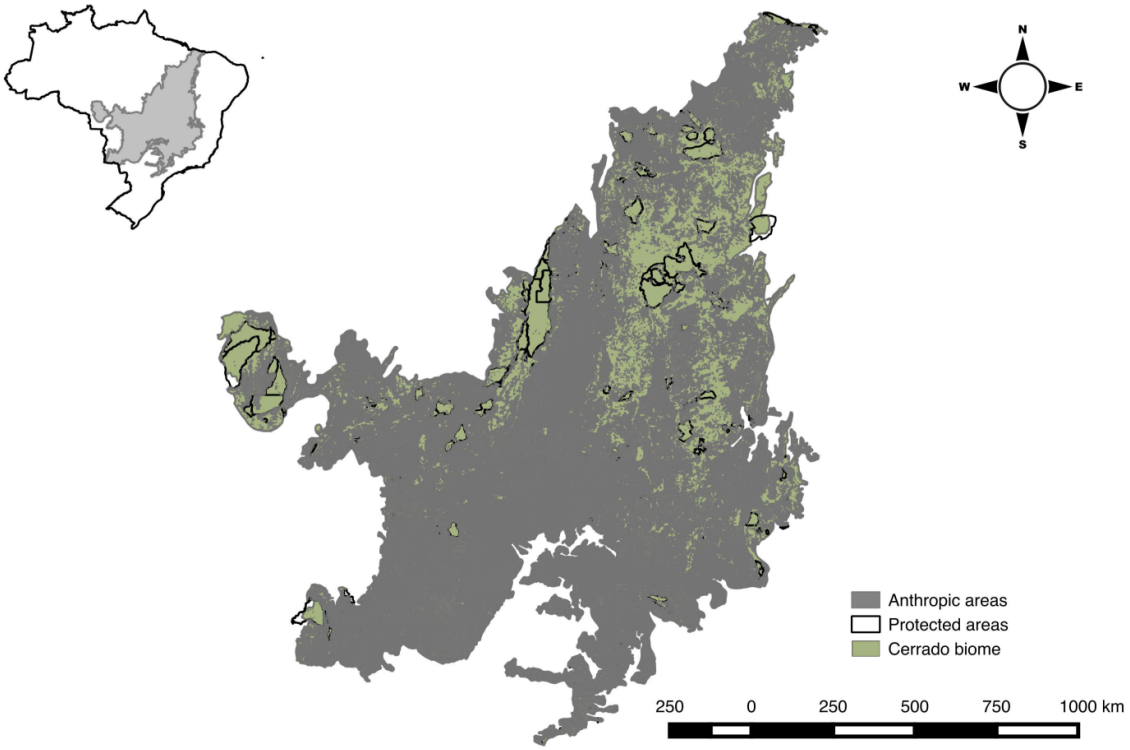

Figure 1.5. Extent of anthropogenic areas in the Cerrado biome (MMA, 2008).

1.4.2. Scientific knowledge and Biases

Unlike forests, grassy biomes have long been viewed as anthropogenic artifacts, degraded lands or secondary successional stages, often neglected by scientists and seen as uninteresting for conservationists (see for example Banerjee, 1995).

In the year 2000, the Cerrado was classified as a global biodiversity hotspot due to high endemism rate and accelerated habitat loss and fragmentation (Klink and Machado, 2005; Myers et al., 2000). Although the extent of the environmental modification is less well documented than the economic transformation, the conversion of the Cerrado landscape is

potentially dangerous for its biodiversity, as 2 amphibians, 24 bird species and 21 mammals are now threatened with extinction in the Cerrado.

Data on the herpetofauna of the Cerrado is still scarce when compared to the herpetofauna of other important biomes and even to other Cerrado taxa (Fig. 1.6). Large areas of this biome were never surveyed (Colli et al., 2002), suggesting that the known species richness is underestimated (Diniz-Filho et al., 2005). Although scientific projects on the Cerrado include studies on natural history (e.g. Alcantara et al., 2007; Durante et al., 2003) and community structure (e.g. Diniz-Filho et al., 2004; Giaretta et al., 2008), information on diversity patterns, habitat use and species distribution is still limited (Colli et al., 2002). Furthermore, data on the influence of the widespread and intensive agricultural practices on the fauna of the Cerrado is rare and often too basic. We searched the literature for original papers published from 1994 to 2014. Searches were carried out in the Web of Knowledge database (apps.webofknowledge.com) in July 2015, using as search terms "Cerrado", ''Amazon'', ''Atlantic Forest'', "Caatinga", ''Pampa" and Pantanal. Afterwards we searched each biome along with ''biodiversity'', "conservation", "agriculture", "amphibians", "mammals" and "birds".

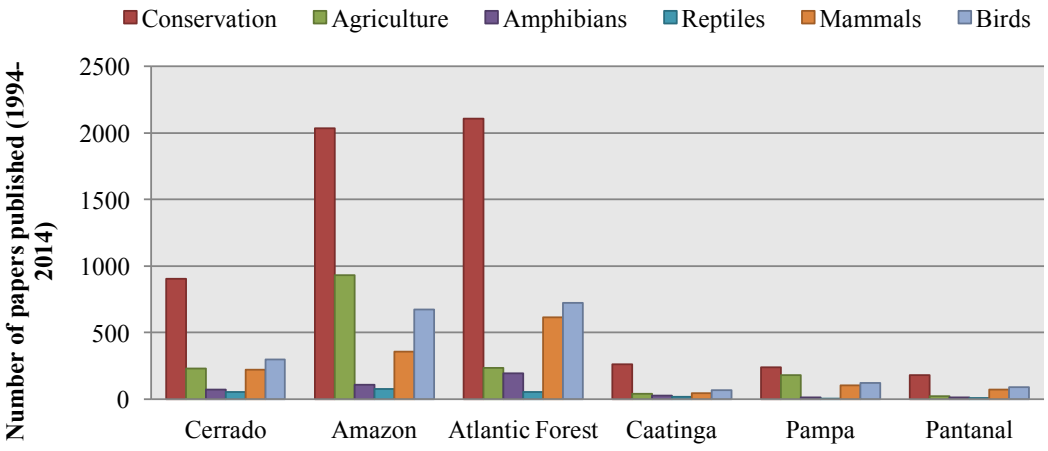

Figure 1.6. Number of papers published on "conservation", "agriculture", "amphibians", "mammals" and "birds" for the 6 Brazilian biomes, from 1994 to 2014.

The Amazon is, by far, the most studied biome regarding every term and all taxa, followed by the Atlantic Forest. The Cerrado is the least studied biome and, among the considered taxa, amphibians are the least studied vertebrates. This trend is especially worrying because of the accelerated degradation of the Cerrado and the global decline of amphibian populations. Research focusing on the biodiversity of the Cerrado has been increasing for the last 20 years, but research focusing on the amphibians of the Cerrado is still incipient (Fig. 1.7), especially considering the anthropogenic pressure on the biome. Furthermore, scientific research on the biodiversity of the Cerrado is extremely concentrated in the southern and central region of the biome (Fig. 1.8), whereas most of the biome has been disregarded probably due to low funding and logistic impairments related to difficulty in sampling highly unaccessible areas. However, according to Valdujo et al., (2012), 19 amphibian species with restricted distributions and/or endemic to the Cerrado are completely unprotected. Therefore, the development of more scientific ecological studies on the anurofauna of this biome is urgent and paramount for the unbiased establishment of conservation policies.

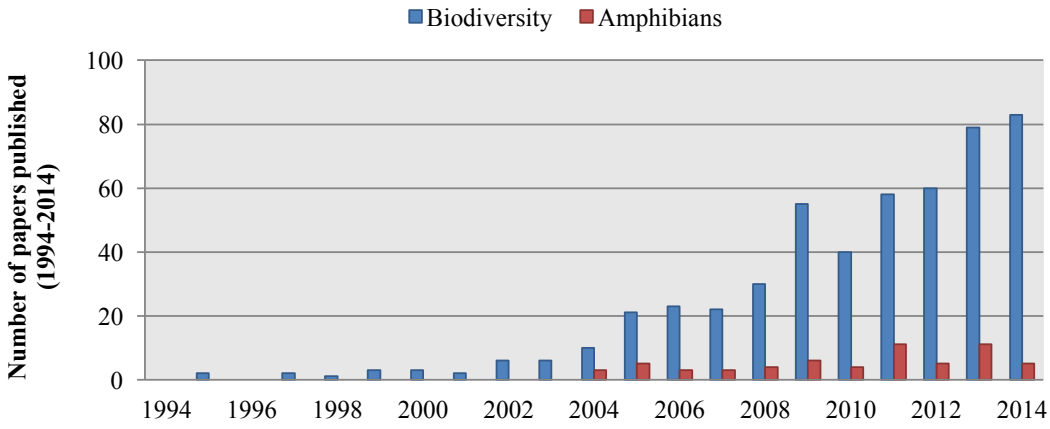

Figure 1.7. Number of papers published on the themes "biodiversity" and "amphibians" regarding the Cerrado biome, from 1994 to 2014.

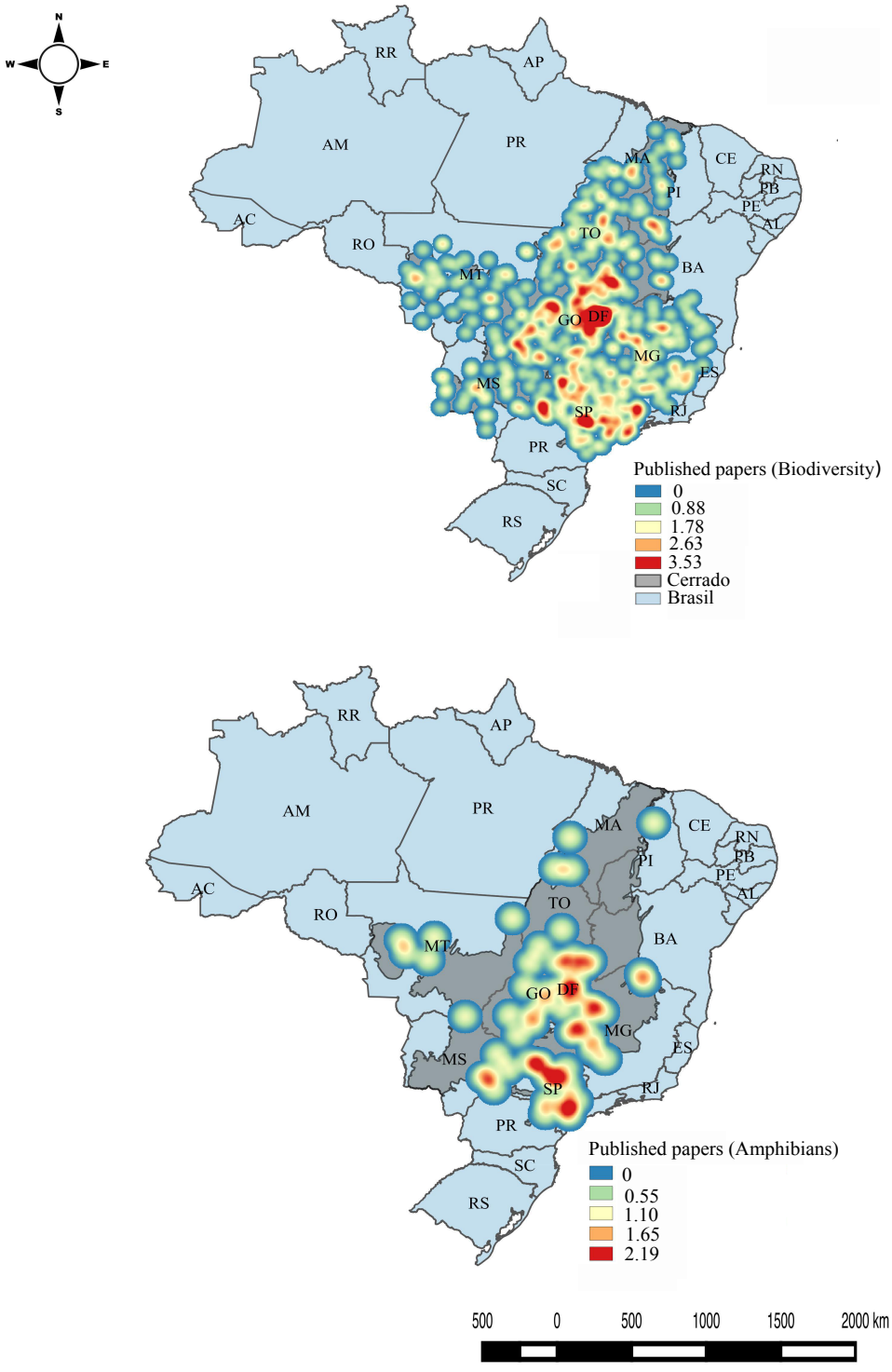

Figure 1.8. Geographical distribution of the papers published on the themes "biodiversity" and "amphibians" from 1994 to 2014.

1.5. Amphibians as surrogate species on ecological assessments

Scientists first became concerned about widespread amphibian population declines at the First World Congress of Herpetology, in 1989. Currently many amphibian species are on the brink of extinction, with 427 species (7.4%) listed as Critically Endangered (CR - the IUCN Category of highest threat), compared with 179 birds (1.8%) and 184 mammals (3.8%) (Stuart et al., 2004). The level of threat to amphibians is undoubtedly underestimated because 1294 species (22.5%) are too poorly known to assess (Data Deficient - DD), compared with only 78 birds (0.8%) (Birdlife International, 2008) and 256 mammals (5.3%) (Stuart et al., 2004). A significant proportion of DD amphibians is likely to be globally threatened (Howard and Bickford, 2014). Analysis of trends in population and habitat availability indicates a deterioration in the status of amphibians since 1980 (Stuart et al., 2004), when 1772 species (31%) would have been globally threatened, including 231 species (4%) in the CR category. Thus, in 1980, the percentage of CR amphibians would have been similar to that of mammals today, but the number of CR amphibians has almost doubled since then. Only 34 species of amphibian are reported to have become extinct since 1500, compared with 129 birds (Birdlife International, 2008)) and 74 mammals (IUCN, 2015). There is strong evidence that this situation is worsening because nine of these extinctions took place since 1980 (compared with five birds (Birdlife International, 2008) and no mammals (IUCN, 2015). Various threats to amphibians, such as global warming, habitat loss, disease vulnerability to chytrid fungus, and pollution) have been identified (Bielby et al., 2006; Kiesecker et al., 2001; Lips et al., 2003; Pounds, 2001; Pounds et al., 2006).

Amphibians have several characteristics that make them useful as indicator species (Heyer et al., 1994). They are often locally abundant (Rocha et al. 2001, Watanabe et al. 2005) and may be sampled with low-cost standard methods (Heyer et al. 1994, Pierce and Gutzwiller 2004). It is likely that amphibians will be good indicators of changes to the whole ecosystem because they are sensitive to changes in the aquatic and terrestrial environments. Aquatic environment is required for reproduction in most species (Duellman and Trueb 1986) and the permeable skin of amphibians makes them sensitive

to water quality and UV radiation in the egg and larval as well as adult life stages (Gerlanc and Kaufman 2005, Taylor et al. 2005). Many amphibian species spend much of their adult life in terrestrial environments, also responding to changes in these environments, especially those affecting water relations through their integument with behavioral responses (e.g., shifting activity periods or moving to different microhabitats) or less frequently with phenotypic responses (e.g., facultative lipid barrier adjustment; Lillywhite 2006).

Some studies use amphibians as indicators of environmental contamination or pollution (e.g. Boone et al., 2007; Egea-Serrano et al., 2009). Others attempt to use the species assemblage (Sheridan and Olson 2003) or relative abundance (Campbell et al. 2005) as indicators of ecosystem health or habitat quality. Amphibians are among the most diverse and abundant vertebrates, play keystone roles in ecosystem functioning, acting as both predators and prey, and enabling nutrient transport between aquatic and terrestrial systems. They are often critical to aquatic and terrestrial food webs, often reaching high densities and biomass (Schiesari et al. 2009). Regarding human societies, amphibians have key roles in disease control, control of agricultural pests (Lajmanovich et al. 2003; Attademo et al. 2005; Peltzer et al. 2005; Attademo et al. 2007; Peltzer et al. 2010), as food source, in pet trade, and medicinal resources (Valencia-Aguilar et al., 2013).

Given their ecological and economic importance, the extent to which threats to amphibians could affect the provision of services should be assessed, especially in the highly diverse and endangered Neotropics. However, the services provided by amphibians have rarely been considered among motivations for acting on their conservation status (Gratwicke et al. 2010). The development of conservation plans for such species and their inclusion in endangered species categories could help protect the ecosystem services provided by these organisms.

1.6. Amphibian dispersal in anthropogenic landscapes

Habitat fragmentation leads to reduced patch size, increased patch isolation, and increased risk of demographic, stochastic and genetic events (Cushman, 2005). This increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Gulve, 1994; Lande, 1988). Spatial and temporal

patterns of animal movement influence population regulation, metapopulation dynamics, and long-term persistence of species (Semlitsch, 2008). Hence, understanding what facilitates and impairs animal movement is pivotal for habitat management and conservation.

Given their biphasic life cycle, amphibians migrate to and from breeding sites, making movement a crucial aspect of population persistence. However, amphibians have lower rates of movement per generation than invertebrates, mammals or reptiles (Bowne and Bowers, 2004). Habitat connectivity has been regarded as key to regional viability of amphibian populations (Cushman, 2005; Rothermel and Semlitsch, 2002; Todd and Rothermel, 2006). Breeding sites lacking connectivity to suitable terrestrial habitat may be population sinks due to high mortality of juveniles during emigration (Rothermel, 2004). Populations may decline if immigration is impaired and may not be recolonized following a local extinction (Semlitsch and Bodie, 1998). Connectivity seems to be of particular importance even in pristine landscapes, as amphibian populations experience relatively frequent local extinction and turnover (Trenham et al., 2003).

In anthropogenic landscapes, the effects of habitat fragmentation on juvenile dispersal are perceived as crucial for conserving pond breeding amphibians (Cushman, 2005). Low recruitment of dispersing individuals probably plays a major role in decline and extinction of amphibian populations in fragmented landscapes (Bulger et al., 2003). There are several important implications of habitat fragmentation on species persistence. High levels of post-metamorphic survival are often required to maintain local populations, but substantial reductions in dispersal success and juvenile survival have been recorded in fragmented landscapes (Cushman, 2005). Hence, habitat fragmentation *per se* can substantially reduce post-metamorphic survival and population connectivity, threatening population viability.

Recently, a number of studies have investigated the relationships between landscape structure and amphibian dispersal. Both spotted salamanders and wood frogs avoid crossing fields, pastures, clear-cuts, lawns, and roads (deMaynadier and Hunter, 1999; Marsh et al., 2004; Regosin et al., 2003; Rothermel and Semlitsch, 2002). Furthermore, orientation of both spotted salamander and wood frog is biased toward forest (Rothermel and Semlitsch, 2002). Lower recapture rates in fields reflected high mortality rates due to desiccation and predation, suggesting that fields are substantially resistant to amphibian dispersal, and thus forest

fragmentation reduces dispersal rates for those species (Marsh et al., 2004; Rothermel and Semlitsch, 2002; Rothermel, 2004).

In order to understand the population-level implications of fragmentation, it is necessary to move from site-specific inferences to assessments of how multiple factors interact across larger spatial extents to influence population connectivity (Bowne and Bowers, 2004; McGarigal and Cushman, 2002). Non-spatial studies conducted at local scales do not provide a basis for inferences at the landscape or regional level (McGarigal and Cushman, 2002). Landscape-level studies that represent the spatial patterns of the environment, addressing species-specific dispersal are essential to extend fine-scale species environment relationships to the population-level (McGarigal and Cushman, 2002).

Understanding amphibian movement is critical for effective management and conservation of amphibians (Rothermel and Semlitsch, 2002), especially in higly fragmented and unstable anthropogenic landscapes. Advances in technology such as radiotelemetry, stable isotope analysis, and use of microsatellite geneticmarkers have yielded greater resolution of the movement ecology of amphibians. However, low funding often impairs the wide use of these approaches. Hence, other techniques have been adopted to study how landscapes shape amphibian meta-population dynamics, such as graph-theoretic approaches. Graph-theoretic approaches may possess the greatest benefit-to-effort ratio for conservation problems that require characterization of large- scale connectivity, due to their ability to provide a detailed picture of connectivity with modest data requirements (Calabrese and Fagan, 2004).

1.7. Objectives and thesis framework

Amphibian ecology is complex, characterized by an inherent duality of dependencies and vulnerabilities, a larval stage associated to waterbodies, an adult stage associated to terrestrial environments and a necessity to migrate to and from waterbodies as recently metamorphosed individuals and as breeding adults. Because of that complex life cycle, approaching how amphibian populations are affected by human-mediated activities demands an integrated, thorough, landscape-scale perspective to reliantly evaluate how populations are shaped by anthropogenic activities.

Although studies spanning many taxa are important for uncovering general and robust relationships between traits and extinction risk (Cardillo et al., 2008), they may conceal important taxon-specific associations. Many species' traits show relationships to extinction risk to be inconciliable across species groups (Purvis et al., 2000), making more narrowly focused studies important (Fisher & Owens, 2004; Isaac & Cowlishaw, 2004; Cardillo & Meijaard, 2012), even though the results may be challenging to generalize.

I attempted to make a multidimensional and integrated evaluation of the effects anthropogenic activities have on the anurofauna of the Cerrado.

In Chapter 2 I revised the literature to summarize the current knowledge on the effects of the main anthropogenic activities on the Cerrado on the biome's anurofauna. I found this important because there is still the misconception that fauna from arid biomes is composed of generalist and resilient species and, therefore, probably not affected by human activities. I also found this review provided me with the ideal position to start assessing how the anurofauna of the Cerrado was, is and will be affected by the anthropization of the biome.

In Chapter 3 I analyzed how anuran species traits related to current official extinction risk and, based on those high extinction risk traits, I predicted the extinction risk for the whole anurofauna of the biome, including species DD. Based on species trait importance, I evaluated conservation targets for every species and propose an integrative framework for assessing species extinction risk and high priority areas for biomes with low funding and high antrohpogenic pressure.

In Chapter 4 I performed and integrative evaluating of the effects of converting natural Cerrado-Amazon ecotone habitats to a vast irrigated rice crop. I assessed taxonomic, functional and phylogenetic diversity and body condition as a metric of population fitness. I also identified which traits are selected and eliminated in Neotropical rice crops.

In Chapter 5 I analyzed how local and landscape features affect overall functional diversity, trait diversity and phylogenetic diversity. I also determined which landscape features are most important for maintaining the most diverse anuran communities in Neotropical agroecosystems.

Finally, in Chapter 6 I approached the connectivity aspect of amphibian populations in anthropogenic landscapes. Using anuran diversity metrics as proxies for amphibian functional

connectivity I evaluated waterbody importance for connectivity in the sampled waterbody network embedded in rice crops. I determined which landscape features are more important for increasing amphibian functional connectivity in Neotropical rice crops.

In Chapter 7 I summarize the main findings from the previous chapters, making management recommendations and presenting priorities for future research projects.

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"Nem tudo o que é torto é errado:
veja as pernas do Garrincha
e as árvores do Cerrado."
Nicolas Behr

Chapter 2

The Anurofauna of a vanishing savanna: the case of the Brazilian Cerrado

2. THE ANUROFAUNA OF A VANISHING SAVANNA: THE CASE OF THE BRAZILIAN CERRADO

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2.1. Abstract

The Cerrado is the second largest biome in Brazil and has been vastly transformed into a highly mechanized and intensive agricultural area, with very little public opposition. The native anurofauna is rich in species number and endemism, but has long been regarded as a generalist community originated from neighboring biomes. The accelerated degradation of Cerrado habitats and consequent landscape fragmentation caused by agricultural activities are invariably bound to affect local anuran communities. However, the effects of these activities on native amphibians are seldom studied, despite the acknowledged adverse effects of these disturbances on the anurofauna elsewhere and the fact that amphibian populations worldwide are declining. This review aims to finally gather the most important findings on the effects of anthropogenic activities on local amphibians. We synthesize the main existing Portuguese and English written literature on the effects of the main anthropogenic activities on the Cerrado anurofauna, generally not easily accessible to the international scientific community. We found a clear paucity of studies on ecology, demography and distribution of the Cerrado amphibians, especially when compared to other biomes and taxa. Yet, the few existing studies indicate that, while this community may be more resilient to some anthropogenic activities (e.g. fire) than their forest counterparts, agricultural environments are strongly dominated by generalist species. Natural forest fragments are important features for maintaining a diverse anuran community in agroecosystems. Intense agrochemical use has been acknowledged to cause

histopathologic alterations and potential decreased fitness. Chytridiomycosis has been recorded in thirteen species extant in the biome, including endemics. The Cerrado anurofauna appears to be especially sensitive to hydroelectric dams, as even previously common, widespread and generalist species declined or disappeared after flooding. Latest predictions indicate that the occupation of the Cerrado will proceed northward, dramatically reducing the proportion of remaining natural habitats due to climate change, leading to a great loss of biodiversity. Only a small portion of suitable natural habitats will remain in northern Cerrado, with amphibian richness being reduced to less than half. Most species will undergo more contraction than expansion of suitable areas in 2050, with high extinction risk. Future climate changes will be especially detrimental for endemic anurans, with small potential current distribution. We conclude that, contrary to widespread beliefs, the biodiversity of the Amazon is not the only one experiencing aggressive threats in Brazil. The anurofauna of the Cerrado is under an unacknowledged extremely high extinction risk and in urgent need of more scientific studies and conservation and management projects.

Keywords: Amphibians; agriculture; fire; rice; soy.

2.2 Introduction

Up to the mid-twentieth century the Cerrado had no economic value and was occupied by a few large extensive cattle farms, as the soil's low nutrient content and acidity, low faunal densities and lack of railroad access restricted agriculture. However, in the 1950's various forms of government incentives stimulated the agricultural development of the biome and transformed it into Brazil's new agricultural frontier. The biome became the country's main source of soybeans and host to the largest cattle herd nationwide (Klink and Moreira, 2002). It is estimated that *ca.* 40% of the Cerrado has already been converted into crops and pastures (Sano et al, 2009), with a cumulative conversion of 43,6% in 2002 and 47,8% in 2008 (MMA/IBAMA/PNUD, 2010) and the highest annual conversion rate (0,7%) of the six Brazilian biomes from 2002 to 2008 (MMA/IBAMA/PNUD, 2011).

Although the bovine herd of the Cerrado was always larger than that of the Amazon, and the percentage of crop area is superior in the Cerrado since 2005 (Fig. 2), the accelerated anthropogenic conversion of the Brazilian savanna has proceeded with little opposition. In fact, this frantic conversion into vast agricultural areas may be a result of international pressure to halt deforestation in the Amazon (Ab'Saber et al. 1990).

Global climate change and a growing human population are expected to increase the frequency and severity of anthropogenic disturbances, which will pose broad effects on biological diversity (McKenzie et al. 2004; Scholze et al. 2006; IPCC 2007). Species response to disturbance depends on the type and magnitude of disturbance, the amount and configuration of remaining habitat, and their life-history characteristics (Prugh et al. 2008; Kuussaari et al. 2009). We aim to summarize the recorded effects of the main anthropogenic activities on the Cerrado amphibians. We will further elaborate on the current decline risk for the biome's anurofauna based on what has been recorded and on the ecophysiological traits characteristic of the biome's amphibians.

2.3 The Cerrado anurofauna

South-American amphibians are concentrated in the Atlantic and Amazon rainforests (Buckley & Jetz 2007). Although savannas are commonly assumed to harbor an impoverished anurofauna (e.g., Duellman 1993), recent studies have uncovered a

surprisingly rich Cerrado, with high anuran species richness (at least 204 species), including endemic, widespread, and marginal species (Valdujo et al. 2012).

The Cerrado is linked to forest biomes and open domains through wide ecotones that favor biological interchange. Communities are thus structured as a mosaic, assembled from multiple adjoining regional species pools (Valdujo et al. 2012). Of the 204 anuran species, 145 are considered typical as they consistently occur in the Cerrado and 59 as marginal, known only from ecotones (Colli et al. 2002). Furthermore, 102 species are endemic or near endemic. Hence, most occurring species are restricted or strongly associated to the Cerrado, while only a smaller proportion is widespread (Valdujo et al. 2012).

Amphibians are ectothermic, have permeable skin and low dispersal ability, resulting in higher ecophysiological constraints (Hillman et al. 2009). As rainfall and temperature determine tropical anuran phenology, the marked seasonality and high spatial heterogeneity of the Cerrado have profound effects on anuran ecology. Accordingly, Cerrado anurans have developed numerous behavioral adaptations to resist desiccation and maximize survival in adverse conditions. Diurnal species of anurans, common in the humid Amazon and Atlantic Forests, are relatively rare in the Cerrado (Heyer et al. 1990). Fossorial behaviors are very common among Cerrado anurans, hiding underground, in holes or under the leaf litter in order to avoid high temperatures and/or low humidity. Breeding strategies are also adapted to the environmental restrictions of the biome as most anurans breed only during the rainy season (October to April) in temporary waterbodies located in open vegetation areas (Brandão and Araujo 1998, Vasconcellos & Colli 2009). *Leptodactylus* sp. commonly dig burrows and build foam nests for their clutch, protecting against predators and facilitating physiological processes such as respiration, excretion and water regulation (Prado et al. 2002, Giaretta and Kokubum 2003, Prado et al. 2005, Kokubum & Giaretta 2005). Foam nests also minimize the increase of temperature and decrease of air/soil moisture in unfavorable conditions such as drought or intense heat, both frequent in the biome.

Although empirically seen as more resilient to anthropogenic practices than their forest counterparts, it is almost certain that, given the magnitude of the ongoing anthropogenic activities, the Cerrado's biodiversity is being affected at ecosystem, community and population levels (see Brooks et al., 2002).

2.4 Effects of the main anthropogenic activities on the Cerrado anurans

The main economic activities in the Cerrado are agriculture and cattle farming. Agriculture has important and complex effects on biodiversity, causing both habitat loss and pesticide contamination, regarded as the main causes for amphibian declines worldwide (Beebee and Griffiths 2005). Agriculture causes spatial and temporal habitat homogenization and decreased suitability of anuran breeding areas (Piha 2006). Crop and pasture setting requires previous land clearing, often with prescribed fires, altering habitat structure, removing the canopy, exposing the floor to sunlight and wind, which leads to a warmer, drier surface microclimate, reducing leaf litter and food resources (Ash 1997, Zheng et al. 2000). These conditions may expose amphibians to warmer and drier microclimate conditions, leading to lower survival or higher evacuation of habitats (Todd and Rothermel 2006, Semlitsch 2008).

Other economic activities, such as hydroelectric exploration, are also prominent in the biome, and cause extensive damage to landscape and biodiversity.

The next section of this review will summarize the main anthropogenic activities occurring in the Cerrado and the studies on their effects on amphibians.

2.4.1 Fire

Fire is an important feature of the Cerrado and its flora and fauna are naturally resistant to it (Coutinho, 1982). However, fire regimes have been tremendously affected by rural activities in the last 20 years. Natural fires occur during the wet season, usually caused by lightning, typically briefer, shallower and colder than prescribed fires. The current main cause of fire in the Cerrado is agricultural and its purpose to transform the native vegetation into crops or pastures (Coutinho 1990). Prescribed fires are hotter and cause increased soil temperature, affecting deeper soil layers. Even in a fire-prone biome, anthropogenic fires may alter soil moisture and temperature, vegetation structure, litter thickness and erosion rates (Schurbon and Fauth 2003).

Drummond (2009) studied the effect of fire on anurans from *campos rupestres*, a fire-prone Cerrado physiognomy (Moreira, 1996), and recorded an increase in species

richness after the fire and an increase in the abundance of the two endemic species of *campos rupestres*, *Physalaemus erythros* and *Scinax curicica*. Although many species were recorded after the fire, every species was represented by only a few individuals. Furthermore, all species found after the fire are known to be resilient to environmental changes such as *Dendropsophus minutus*, *Scinax squalirostris*, *Scinax fuscovarius*, *Leptodactylus latrans, L. fuscus and Rhinella pombali* (IUCN 2013). The author also found a higher frequency of terrestrial species, often considered more resistant to fire than arboreal species (Friend, 1993), as they remain buried during the dry season.

The burying habit has been recorded for several Cerrado anurans such as *Physalaemus sp.* (Santos et al., 2003) and *Leptodactylus sp.* (Oliveira Filho et al., 2005). These species also build foam nests, known to prevent clutch desiccation and provide thermal stability (Dobkin & Gettinger, 1985). These fire-resistance features, common in savanna amphibians, may explain the increased abundance of terrestrial species after fires, especially when compared to forest communities.

Despite also being considered resistant to anthropogenic disturbances, *Ischnocnema juipoca* was abundant throughout the area before the fire, but rarely found afterwards. Species of *Brachicephalidae*, such as *I. juipoca*, are completely terrestrial, have direct development and find shelter at the base of grass clumps (Eterovick and Sazima, 2004). Consequently, once the vegetation of the area was swept by fire, mortality of *I. juipoca* was likely substantial. Furthermore, this species may lays its eggs at the base of grass clumps, due to the higher water availability (Eterovick and Sazima, 2004), but in a soil devoid of grasses and exposed to desiccation, reproductive success may be low in environments recently burned. Hence, *I. juipoca* may be especially susceptible to fire despite its association to a fire prone phytophysiognomy.

The author also detected an increase in microhabitat use and inter-specific competition in arboreal anurans after the fire. This can be associated with the destruction of preferred microhabitats available in marginal and aquatic vegetation, suggesting the use of sub-optimal microhabitats by this group after the fire. Arboreal species showed a large proportion of empty stomachs, smaller prey and lower total volume of prey compared to terrestrial species. These results confirm those by Rocha et al. (2008), who found a negative effect of fire on the diet of *Scinax* sp..

Amphibians are carnivores with a diet composed mostly of arthropods (Araújo et al., 2007; Almeida-Gomes, 2007). Fire may have negatively affected the arthropod community, reducing prey availability for amphibians. While treefrogs were negativelly affected, terrestrial species seemed unaffected because arthopods such as termites and ants build underground nests and resist fires (Vasconcelos et al. 2008), being available as prey to terrestrial frogs. However, arboreal anurans are unlikely to forage on terrestrial preys.

These results were corroborated by Brasileiro (2004), who found anuran species richness and abundance to be unaffected by fire and higher interspecific competition for calling and egg-laying sites following the elimination of emergent vegetation by fire. Morais, Côrtes and Bastos (2011) studied the influence of fire on co-occurrence patterns of anurans in *veredas*, linear environments associated to watercourses (Oliveira & Ratter, 2002), composed of hydrophilic vegetation and characterized by a dense herbaceous layer and dominance of the arboreal palmtree *Mauritia flexuosa* (Ribeiro & Walter, 2008). The authors observed that co-occurrence patterns, anuran species composition and richness were not significantly influenced by fire.

Fire-induced vegetation changes can increase water temperature, alter water holding capacity of plants and soil and lead to changes in the timing of peak and low-water events (Rieman and Clayton, 1997). Thermal stress and rapid changes in water chemistry may cause mortality of some species in ponds or streams (Spencer and Hauer, 1991). However, tadpoles of some Cerrado anurans are known to be resilient to several environmental changes. Larvae of *Scinax fuscovarius* and *Leptodactylus fuscus* tolerate high water temperature (Schinia and Neto, 1990), and low oxygen levels, which may be common in waterbodies with sparse vegetation. Eterovick & Sazima (2000) argue that the same can happen for tadpoles of *Leptodactylus cunicularius, Leptodactylus furnarius* and *Physalaemus cuvieri*. In fact, intense fire in watersheds can result in increased concentrations of nutrients such as phosphorus, ammonium, nitrate, and nitrite in waterbodies, which may increase the productivity of aquatic ecosystems, providing more food and, therefore result in faster growth of resilient herbivorous anuran larvae (Kiffney and Richardson, 2001).

Despite their ecophysiological constraints, the main effects of fire on amphibians are most likely indirect, as fire often creates an inhospitable environment associated with profound alterations to the leaf litter, ground cover, and soil. Loss of cover can result in

exposure to extreme temperatures, desiccation, high predation risk, physiological stress and reduced dispersal and foraging abilities. Several studies (e.g. Cano & Leynaud, 2010, Matthews et al., 2010) found negative effects of fire on anuran assemblages and suggested that fire may reduce species richness and abundance. However, and despite the paucity of studies, it appears that species native from grassy biomes exhibit some remarkable resilience to burning due to behavioral traits and reproductive strategies. Nonetheless, some species may be especially threatened.

Vulnerability to fire varies as forest communities may be especially sensitive (Gardner, Barlow and Peres, 2007), while savanna communities such as the Cerrado may be more resilient. Nevertheless, long-term studies must be developed to clarify the effects of fire on the diverse Cerrado anurofauna, especially regarding anthropogenic fires (Morais, Côrtes and Bastos, 2011) and the effects of altering fire regimes from superficial, lighting-caused, rainy season fires to more aggressive, anthropogenic fires set during the dry season.

2.4.2 Crops

The influence of agriculture on amphibian populations has been reported for many regions (e.g. Beja and Alcazar 2003). Agricultural activities are varied in nature, timing and gravity for biodiversity. Overall, effects are complex and dependent on characteristics such as timing, vegetation structure and cover, species cultivated, plant density and row-spacing. Habitat loss, decreased connectivity and water contamination are the most conspicuous effects of agriculture on amphibians worldwide (Liner *et al*. 2008). However, the potential an activity has to be detrimental to amphibians depends on the nature of the activity, how directly the amphibians are exposed to it and on the ability amphibians have to resist or escape the threat. Naturally, activities that occur during the time period amphibians are more active have higher probability of affecting amphibians than activities occurring on a period during which amphibians are not vulnerable (Fig. 2.1). Hence, when analyzing how anthropogenic activities may affect biodiversity, it is pivotal to consider species characteristics.

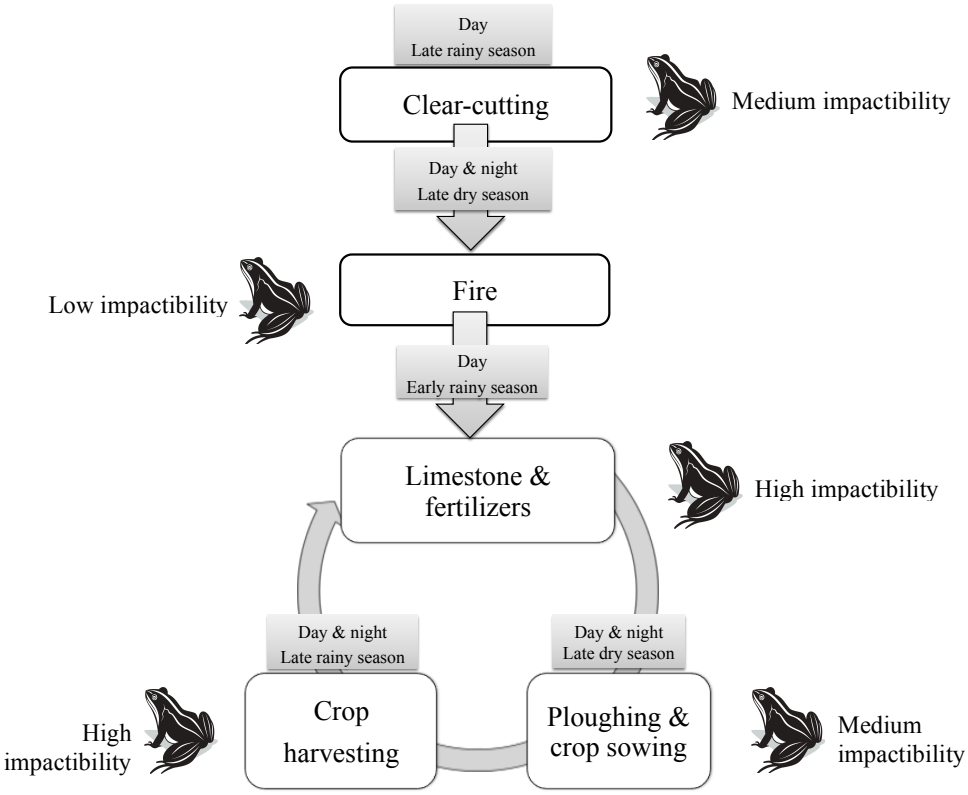

Figure 2.1. Most common process of agricultural exploration in the Cerrado and perceived impactibility of each activity on amphibians, based on seasonality and periods of more activity.

Despite the ecological value of the world's most diverse savanna, and the omnipresence of human-mediated activities on the Cerrado, few studies have addressed the influence of agriculture on the biome's anuran communities.

Among the main crops of the Cerrado, soybean and rice originate different microclimatic conditions, distinct resource and refuge availability, posing different survival risks for local anurans (Fig. 2.2). The conversion of native Cerrado habitats into soybean crops and rice fields causes a significant reduction in evapotranspiration and an increase in water flow (Nosetto et al. 2011). In denser crops, with smaller row spacing, soil temperature may be lower than in soils covered by native vegetation and leaf litter less abundant and more homogeneous in crops. Furthermore, in the Cerrado, crop plantation often occurs when anurans are most active (beginning of the rainy season), which may be especially detrimental to individuals migrating from hibernation shelters to breeding sites.

Once again, studies on the effects of the main cash crops of the Cerrado on anuran communities are very scarce, but we will describe the results of the most important works on this subject.

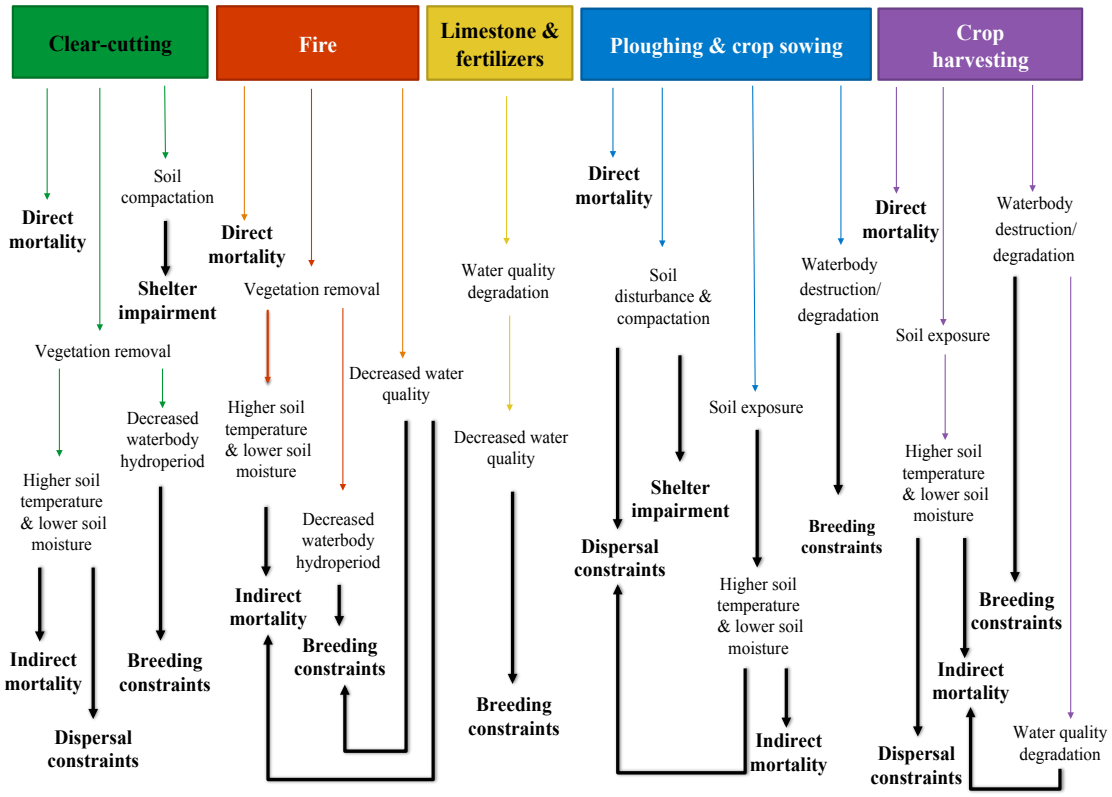

Figure 2.2. Consequences of the main activities involved in most agricultural activities, with possible consequences for the anurofauna present in agro-environments. Environmental consequences of each activity are represented as colored arrows, effects on amphibians are represented as black bold arrows.

2.4.2.1. Soy crops

Silva et al. (2009) assessed the anuran community in agro-systems and found only terrestrial species in soy crops (*Leptodactylus mystacinus*, *Physalaemus cuvieri* and *Physalaemus nattereri*). *Physalaemus nattereri,* a burrowing frog (Freitas et al., 2001), was the only species found in all crops, perhaps because it can remain burrowed until the following reproductive season, escaping many of the disturbances. According to Gray et al. (2004), agricultural disturbance around wetlands may positively influence the abundance of some amphibian species. Less vagile amphibians that aestivate and breed explosively are competitively dominant in the absence of predators and may benefit from landscape cultivation (Gray et al. 2004). Agricultural landscapes may therefore have a negative influence on anuran communities, causing decreases in species richness or favoring the occurrence of generalist species as a result of changes to the vegetation.

Vaz-Silva (2009) found that areas distant from monocultures showed higher tadpole heterogeneity, species richness and abundance of treefrogs. Furthermore, microhabitat availability was higher in waterbodies distant from crops, providing more calling sites and refuges for adults and larvae. Overall, *S. fuscovarius, Dendropsophus minutus* and *E. nattereri* were the most abundant species but, while *E. nattereri* was common in smaller, colder, shallower waterbodies located close to crops, tadpoles from *D. minutus* were associated with larger, warmer, deeper, with low pH waterbodies, distant from soy crops and closer to forest fragments. Microhabitat use was higher in agricultural environments and most species found in both pristine and agricultural waterbodies had smaller niches in agricultural waterbodies. In areas distanced from the crops, *D. minutus* and *S. fuscovarius* displayed wider niches, suggesting great environmental plasticity regarding microhabitat use. In areas near crops, *E. nattereri* and *L. fuscus* behaved as generalist species, with broad niches.

Morais et. al. (2011) found species richness in waterbodies located near soybean crops to be high and similar to that of protected areas in the biome (Eterovick and Sazima 2004, Uetanabaro et al. 2007). However, most of the recorded species were widespread (Frost 2010), open area breeders and habitat generalists (Brasileiro et al. 2005).

Campos et al. (2013**)** found higher species richness and abundance in temporary lentic waterbodies on an agricultural matrix, corroborating previous studies (e.g. Prado et al. 2005, Santos et al. 2007, Vasconcelos et al. 2008). Structural habitat heterogeneity and larval development plasticity account for the increased species richness and relative abundance in temporary ponds compared to lotic waterbodies and permanent lagoons. Diverse vertical strata favors a wider array of species, including hylids, leptodactylids and leiuperids, whereas lotic waterbodies typically have less diversified marginal vegetation and favor a smaller array of species commonly with strong breeding specializations. However, lentic temporary waterbodies harbored many generalist species associated to anthropogenic environments.

2.4.2.2. Rice crops

Despite the modifications ensuing the replacement of native vegetation by rice crops and the alterations to the hydrological cycle resulting from irrigation techniques, rice fields often harbor many species (Elphick 2004; Doody et al. 2006) and have been considered "functional equivalents" to natural wetlands (Elphick 2000).

Given the actual expansion of rice crops in the Neotropics, and particularly in the Cerrado, it is important to determine if agricultural wetlands can maintain high levels of biodiversity. Several studies have analyzed biodiversity patterns in fragmented wetlands in Brazil (Stenert and Maltchik, 2007; Rolon et al., 2008; Stenert et al., 2008), but the importance of rice fields to the conservation of Neotropical amphibians has been overlooked. Since wetlands serve as important breeding sites for most amphibians, alterations to these systems can compromise several anuran species (Silvano and Segalla, 2005).

Irrigated rice fields in Brazil present a dynamic hydrologic regime, with variation between aquatic and terrestrial phases, remaining without surface water during the fallow phase, when the crop is drained and rice sowed. Despite rice being one of the main cash crops of the Cerrado, there are no studies on the effects of rice crops on anuran communities.

Duré (2008) studied the anuran community of irrigated rice fields in the Argentinian savannah and found a diverse anurofauna similar to that found in undisturbed wetlands, as was previously recognized by Bambaradeniya *et al.* (2004). However, they also found that natural vegetation supported the highest species richness. This underscores the importance of retaining patches of natural vegetation in rice paddies to maintain diverse anuran communities. Earthen irrigation ditches also assure conditions for diverse anuran microhabitats, especially useful for dispersal from natural vegetation into flooded rice fields. Bambaradeniya *et al*. (2004) found that aquatic organisms were able to use dry rice field soil cracks and crevices for aestivation when the fields were drained. This finding is corroborated by Duré (2008), who found adults and foam nests in cracks after field drying. Perennial pools with aquatic vegetation may explain the presence of frogs in rice fields and indicate the importance of such features for anuran populations. The existence of aquatic species, such as *Lysapsus limellum,* in an environment subjected to drastic water levels variations was also of interest. The existence of pools that contain aquatic vegetation throughout the terrestrial dry phase, would explain the presence of these frogs.

Machado and Maltchik (2010) investigated the potential role of rice fields as refugia for amphibians and how different management practices could influence the amphibian community. Twelve anuran species were found in the rice fields, representing 75% of the area's species richness (Loebmann, 2005). However, species composition in pristine wetlands differed from that found in rice fields, mainly regarding the dominance of hylids and leptodactylids. Furthermore, anuran richness and abundance changed over the rice cultivating cycle, peaking in the growing phases, during the warmer summer, with abundant surface water. This study showed that even though management practices in rice fields produced similar anuran richness and abundance, species composition is different from pristine areas. Lack of surface water in dry rice fields during most of the cultivating cycle favored the development of terrestrial species, such as Bufonidae, Cycloramphidae, and Leptodactylidae whereas in rice fields that remained flooded, hylids were more abundant. Hence, the mosaic created by rice wetlands and drained lands can harbor high anuran diversity but rice fields must not be viewed as surrogate systems for natural wetlands, given that the more complex natural systems harbor more diverse communities, influence aquifer recharge, climatic stability and water storage.

Moreira et al. (2014) recorded 60% of region's total species richness in rice fields, with dominance of open areas species. Indeed, it has been argued that only generalist species are able to remain in areas converted to rice fields (Doody *et al.* 2006; Piatti *et al.* 2010). Amphibians that depend on ponds in agricultural fields may be exposed to high levels of agrochemicals, which could affect biota directly or indirectly (Peltzer *et al.* 2008; Attademo *et al.* 2011). Agricultural intensification also affects the structure of habitat in which amphibians forage and reproduce (Peltzer *et al.* 2006; Piatti *et al.* 2010). Non-specialized reproductive modes (*e.g*. mode 1 *sensu* Haddad and Prado 2005) or those that confer some protection against desiccation (*e.g.,* modes 11 and 30) are more favored in open areas or environments with seasonal availability of water, such as rice fields. Temporary environments are more likely to dry up and be occupied by species with rapid development and those that build foam nests, which allow the larvae to survive until the next rain/flood (Zina and Haddad 2006). Indeed, the authors found a higher number of tadpoles of species that deposit eggs in foam nests inside subterranean constructed chambers (mode 30). Despite rice fields being often perceived as potential surrogate habitats for many wetland species (Machado and Maltchik 2010), tadpole abundance was low. Although the presence of tadpoles might be a good indicator that rice crops are effectively used for breeding activity, this must be heeded cautiously, as tadpoles might have originally occurred in other flooded areas and then ended up in the rice fields via irrigation water. Fish that generally prey upon tadpoles were observed inside rice quadrats and irrigation channels, which, in addition to the predation effect on tadpoles and adults, influences breeding site selection by amphibians (Werner *et al.* 2007). Additive or synergistic effects of pesticide use and habitat homogenization on tadpole predation have been demonstrated in amphibians (Mann *et al.* 2009). Thus, fish predation associated with low tadpole abundance could explain species absence during the late growing period. The authors also found hylid tadpoles in organic rice fields, which may be associated with the presence of a strip of vegetation close to these rice plots. During the off-season, organic crops retain water in the irrigation and drainage canals, ephemeral pools are common in the rice plots. Conventional fields are drained and sometimes used for cattle grazing. It has been suggested that hydroperiod predicts tadpole guild composition in grasslands (Santos *et al.* 2007; Both *et al.* 2011). In this case, presence of hylid tadpoles in organic fields might simply be related to longer hydroperiods. However, this does not exclude other

effects of organic management, such as no or little use of chemical pesticides/inorganic fertilizers and maintenance of a heterogeneous landscape around crop edges, of contributing to abundance in nearby areas.

Maltchik et al. (2011) investigated if irrigation channels could maintain high anuran diversity over the cultivation cycle and found species corresponding to 63% of the richness observed in the studied region (Loebmann 2005). However, anuran community was strongly dominated by *L. latrans*, *P. minuta*, and *P. biligonigerus*, all generalist and highly adaptable species (Loebmann 2005).

Crops can maintain apparently viable anuran populations despite the fact that the main anuran breeding and feeding season may occur during cropping. However, there will be a dominance of generalist, widespread, open area breeders and terrestrial species. In particular, rice fields appear to have the potential to support diverse anuran communities, due to certain characteristics of rice production, namely the need to flood the crop. However, natural vegetation fragments, earthen irrigation channels and shallow depressions that support perennial ponds and aquatic vegetation must be assured as they appear to be important landscape features for promoting the use of rice fields by anurans. Nonetheless, even if these structures are assured in agricultural landscapes, anuran populations of generalist species might be under sup-optimal conditions. Telles et al. (2007) analyzed the genetic structure of *P. cuvieri* populations from central Cerrado and found that anthropization explains patterns of genetic distances, even regarding recent disturbances. The genetic distances found were higher than expected by geographic distances. Current human population density, characteristics of habitat fragmentation and year since the creation of each municipality are involved in the explanation of these discontinuities. Indeed, the southeast region of the biome, with the strongest discontinuities, was the first region occupied, in the 18th century.

2.4.3 Agrochemicals & Diseases

Besides habitat degradation and fragmentation, contamination from agrochemicals is the biggest threat to amphibians worldwide. Although Brazil is the world's largest consumer of pesticides (Pacheco, 2009), the impacts of agricultural pesticides on local amphibians have barely been explored. The most commonly used herbicides in soy and rice crops are glyphosate, phenoxyacetic acid (2,4-D) and endosulfan.

Simioni, Silva and Mott (2013) determined the toxicity (CL_{50}) of the herbicide glyphosate on *P. albonotatus* and tadpole survivorship rates under sub-lethal concentrations. Glyphosate is a systemic herbicide, considered slightly toxic to vertebrates and environmentally innocuous since it is promptly adsorbed and does not remain active in the environment. However, some studies have indicated that glyphosate can cause negative impacts to the biota (Langiano & Martinez, 2008), including amphibians (Releya, 2005; Releya & Jones, 2009). The CL_{50} value for *P. albonotatus* was four times smaller than the value found for a congeneric species (*P. centralis*) using the same protocol (Figueiredo and Rodrigues, 2010). Figueiredo and Rodrigues (2010) found even higher values of CL_{50} for two other Brazilian amphibian species, the bufonid *Rhinella marina* and the microhylid *Elachistocleis sp*. These discrepancies may reflect a differential resistance of anurans species to herbicides. Figueiredo and Rodrigues (2010) collected egg masses in puddles close to soybean plantations, where glyphosate has been used for at least a decade. Anuran species with different historical contact with pesticides may develop tolerance. Species-specific tolerances may also be due to phylogenetic factors or environmental conditions and merit further investigation, as there was also considerable variation in the response of Brazilian anuran species to sub-lethal concentrations of glyphosate. For example, *P. centralis* had higher mortality rates when kept in higher sub-lethal concentrations of glyphosate. For *R. marina*, 50% and 75% of CL_{50} also affected survivorship, although for *Elachistocleis sp.* differences in mortality among different sub-lethal concentrations were not statistically significant (Figueiredo and Rodrigues 2010). Hence, glyphosate exposure poses different threat levels to different anuran species. However, further research is needed to assess whether resistance is influenced by phylogenetic signature, tolerance and/or historical contact with pesticides.

Moreira et al. (2012) analyzed groundwater and rainwater for pesticides and related these data to morphological anomalies and presence of organochlorines in the blood plasma of *R. schneideri* and *Leptodactylus labyrinthicus*. Residues of endosulfan, flutriafol and atrazine were detected in the water. Endosulfan, an organochlorine insecticide, is known be very toxic to aquatic and terrestrial organisms (Grisolia, 2005) and many studies have confirmed its mutagenicity, teratogenicity and carcinogenicity (e.g., Gupta, Saxema and Chandra, 2000). Endosulfan residues were detected in the plasma of *R. schneideri* and *L. labyrinthicus*. Posterior analyzes detected external malformations in cane toads but not

in pepper frogs. The presence of residues of endosulfan and others organochlorine pesticides in anuran blood plasma may indicate impaired fitness, as atrazine is known to cause loss of larval swimming performance, adult sex changes and various anatomical anomalies.

Lima (2010) performed histological analysis on liver, skin and reproductive system of *Leptodactylus latrans* individuals from pristine and agricultural Cerrado areas. Although both liver and skin showed histopathologic changes, liver tissue was damaged in animals from pristine and agricultural areas. Two of the three studied areas where under direct influence of agriculture, but the first area was presumably free of pesticides, which may indicate the power that pesticide use in agricultural areas have on the surrounding habitats.

Survival in agroecosystems depends upon the physiological tolerance of organisms to adapt to rapid changes in the habitat or to adopt an effective dispersal behavior (Beja and Alcazar 2003; Bambaradeniya et al. 2004; Davidson 2004). The available studies indicate that the generalists commonly found in Cerrado crops may be in sub-optimal fitness conditions due to pesticide exposure, representing an inconspicuous detrimental consequence of agriculture for anuran populations. More studies are urgently needed in order to thoroughly assess the effects of agrochemicals on the Cerrado anurofauna.

Infectious diseases in general are regarded as one of the most significant catalysts driving global amphibian declines (Young 2004), and the emerging chytridiomycosis is a prominent cause of anuran population declines (Schloegel et al. 2010). Chytridiomycosis, caused by the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), has been detected in more than 350 amphibian species (Skerratt et al. 2007, Lips et al. 2006, Stuart et al. 2004). This disease has been linked to population decline in at least 200 species since 1980 (Skerratt et al. 2007). The fungus targets amphibian skin and colonizes keratinous structures such as tadpole oral discs (Berger et al. 1998). Infections in tadpoles can affect their feeding, constraining growth, metamorphosis, and survival (Blaustein et al. 2005). During metamorphosis the skin becomes more keratinized, allowing the fungus to potentially spread to other parts of the body (Rachowicz et al. 2004, Berger et al. 2005, De Paula & Catão-Dias 2011). In adults, the infection induces skin hyperkeratosis and slough off (Berger et al. 1998). The hyperkeratosis alters proper osmotic regulation, causing some individuals to suffer from a hydroelectrolytic imbalance and subsequent death due to a heart attack (Voyles et al. 2009, Campbell et al. 2012).

In Brazil, *Bd* has been recorded in species belonging to ten anuran families from the Atlantic Forest (Becker & Zamudio 2011, Carnaval et al. 2006, Grundler et al. 2012, De Paula & Catão-Dias 2011, Ron 2005, Schloegel et al. 2010, Toledo et al. 2006a, Toledo et al. 2006b). Ramalho (2015) recorded the first case of *Bd* in amphibians from the Cerrado and also for species of the endemic *Bokermannohyla pseudopseudis* group. These species occur in small geographic ranges at high altitudes (above 900m a.s.l.), and their tadpoles develop in low-temperature, fast-flowing streams and rivulets (Eterovick & Brandão 2001, Brandão et al. 2012). These traits may increase species susceptibility to chytrid infection (Rödder et al. 2009), as there are several reports of chytrid fungus causing infection of stream dwelling species (Piotrowski et al. 2004, Lips et al. 2003, La Marca et al. 2005). Climate conditions in the Cerrado seem suitable for the survival and spread of the pathogen, and some models have already predicted the occurrence of *Bd* in the biome (Ron, 2005, Toledo et al. 2006b). Thirteen species extant in the Cerrado have been found infected by *Bd*, although diagnoses were confirmed on populations from other biome. Hence, more *Bd* studies are urgent for this biome and potentially susceptible endemic species from rupestrian habitats.

2.4.4 Cattle pastures

The Cerrado is host to 42% of the national bovine herd and 67% of the biome's total cleared land has been used to set pastures. Native grasslands are clear-cut, burned and seeded with potentially invasive African grasses (Klink 1994) to form cattle pastures. Open area anurans are often seen as generalists with reproductive strategies adapted to harsh conditions (Haddad and Prado 2005) and some species may be resilient or even thrive in pastures. However, despite being regarded as innocuous and even beneficial to amphibians given the seemingly mild practices and presence of waterbodies used as breeding sites, studies on the effect of pastures on anurans are still insufficient to achieve that conclusion.

Silva, Candeira and Rossa-Feres (2011) evaluated which pond characteristics affected anuran species occurrence in farmland ponds located in a pasture matrix. They found 26 anuran species, but only *Leptodactylus fuscus*, *E. nattereri*, *Pseudopaludicola falcipes* and *P. cuvieri* were consistently found, whereas most species were recorded in

only one or two ponds. According to this study, anuran species richness in farmland ponds is mainly predicted by marginal vegetation height and other variables related to habitat heterogeneity that reflect the structural complexity of breeding sites. The occurrence of *Boana albopunctata* was associated with higher aquatic vegetation heterogeneity, whereas the occurrence of *Elachistocleis cesarii* was associated with a greater vegetation cover in the pond surface. The occurrence of *E. nattereri* was associated with lower aquatic vegetation inside the pond, whereas the occurrence of *L. podicipinus* was associated with taller marginal vegetation. *Leptodactylus fuscus* occurred mainly in ponds showing intermediate or permanent hydroperiods whereas *P. falcipes* was associated with large ponds and ponds with taller aquatic vegetation.

De Marco et al. (2013) investigated local and regional patterns of species richness in the Cerrado ponds and found that amphibians were affected by environmental gradients related to water parameters, being positively affected by increased chlorophyll, ammonium, pH, and electric conductivity and negatively affected by increased transparency, representing mainly the trophic state of the pond. Several studies previously conducted in tropical and temperate regions have found that anuran species richness is positively correlated with the amount and/or diversity of vegetation within ponds (Burne and Griffin 2005; Lichtenberg et al. 2006; Silva et al. 2011) and in pond margins (Hazell et al. 2004; Peltzer et al. 2006). The importance of marginal vegetation height for species richness is related to the greater diversity of microhabitats provided by different levels of vertical stratification, allowing a greater number of species to coexist.

Silva, Gibbs and Rossa-Feres (2011) evaluated the effects of environmental variables on anuran species richness and abundance in artificial temporary pools located in a pasture matrix. Although they recorded 27 anuran species, only *P. cuvieri* and *L. fuscus* were recorded in every pool, whereas most species were found in only one pool.

Pools with longer hydroperiods and more aquatic vegetation supported higher species richness. In areas with long and intense dry seasons, unpredictable rainfall and predator pressure promote the use of long-term temporary habitats for amphibian reproduction. For most species, breeding occurs during the rainy season (October to March) so it is probably most advantageous to colonize temporary breeding pools with longer hydroperiod, where there are few predators, than to occupy either short-hydroperiod sites, such as breeding pools that may be free from predators but have high risk of desiccation, or permanent pools

with elevated numbers of predators (Wellborn et al. 1996). Aquatic vegetation was especially important for arboreal species that vocalize perched in the vegetation. Pools with more structural complexity may be more inviting for anuran reproduction because they offer more sites for calling, amplexus, and oviposition, as well as shelter for recently metamorphosed tadpoles and adults from predators (Shulse et al. 2010).

Distance from the pool to the nearest forest remnant was also determinant for some species, especially *E. bicolor* and *E. nattereri*, two small burrowing frogs that have low dispersal capacity (Silva and Rossa-Feres 2011). Discontinuity between suitable aquatic and terrestrial habitats, a phenomenon known as "habitat split", forces many species with aquatic larvae into risky breeding migrations through disturbed environments (Becker et al. 2010) and may result in population extinction. Forest fragments have been identified as important habitats, providing refuge for many arboreal and fossorial species (Hazell et al. 2001) and enhancing landscape connectivity (Becker et al. 2010). Silva et al. (2012) studied the effect that landscape configuration had on anuran abundance and diversity in agro-savanna landscapes. The authors found that generalist species used both pasture and forest habitats and were forced to cross open habitats to reach cattle ponds to breed, despite the inherent risks of crossing pastures (Urbina-Cardona et al. 2006). Ponds closer to fragments had higher anuran abundance and species richness than those far from or even within forest fragments. This study indicates that landscape configuration has an important influence on anuran population viability in tropical agricultural landscapes

Silva and Rossa-Feres (2011) analyzed how anuran species richness varied in waterbodies located in a pasture matrix with increasing distance from forest fragments. They found that the dominant species were the same regardless of the pools' distance from the forest fragments. However, species were more abundant and showed prolonged breeding activity in pools closer to forest fragments. Forest fragments facilitate anuran migration from breeding, to feeding and aestivating areas (Silva & Rossa-Feres 2007) and are increasingly important as altered environments may impair anuran movement (Becker et al. 2007). These results reinforce the importance of forest fragments even for open area breeders. Several temperate-zone studies recorded higher anuran richness in breeding pools near forest fragments than those without nearby forest fragments (Herrmann et al. 2005). In contrast to these studies, where species composition was a mix of forest-associated and open-habitat species, the species recorded by Silva and Rossa-Feres (2011) are typical of

open areas and tolerant to anthropogenic modifications (Duellman 1999). The higher temperature and lower soil moisture typical of open areas are known to restrict the occurrence of anurans, which experience higher rates of evaporative water loss and mortality due to desiccation or increased mortality from predators (Rothermel & Semlitsch 2002). Consequently, proximity of breeding pools to forested patches and more suitable micro-climatic conditions enable some species to extend their breeding activity compared to breeding pools distant from them. These studies emphasize the importance of forest fragments and indicate that conserving these fragments is paramount for amphibian diversity and abundance in tropical agro-savanna landscapes, even for open area breeders.

2.4.5 Hydroelectric exploration

River damming and the creation of large reservoirs are among the severest and most permanent human interferences on nature (Tundisi 1996). Flooding due to a hydroelectric dam causes habitat loss and fragmentation, population isolation, and reductions in species richness, abundance, and movement patterns. The Cerrado is the birthplace of the rivers that originate Brazil's six main watersheds (Parnaíba, Paraná, Paraguai, Tocantins-Araguaia, São Francisco and Amazonas), making the biome's potential for hydroelectric dams very high.

Although this is a much unaddressed issue, Brandão & Araújo (2008) studied changes on anuran abundance and richness caused by habitat loss and insularization during the flooding of the Serra da Mesa hydroelectric reservoir, in Central Brazil, created by the damming of Tocantins river. The enormous area flooded (178,000 ha) was previously covered by several phytophysiognomies but after complete flooding only 280 islands were formed by the isolation of hilltops. After complete flooding, only 11 of the 31 species originally found were still recorded on the site. *R. schneideri*, a large, abundant, and generalist species, commonly found in human-modified Cerrado habitats, almost disappeared from the islands during the following months. *P. cuvieri* and *Rhinella granulosa* were the most abundant species on the hills before flooding but showed significant declines in abundance after insularization. All amphibian species that depend on the availability of water bodies went extinct on the islands. Species that used gallery forests, previously present on the lowlands, went extinct as the gallery forests of the region were submerged. Despite the fact that most species of Serra da Mesa use lentic habitats,

the number of species found at the end of the study corresponds to less than 30 percent of the total number of species recorded in the region before dam formation.

It was expected that opportunistic species would be favored with the flooding and the creation of a new permanent aquatic environment. However, this study shows that hydroelectric reservoirs located in the Cerrado are not used by most anurans as reproductive sites. In fact, only *R. schneideri* used the lake for reproduction, while other generalist species were not observed breeding in the lake. Besides the presence of predatory fishes, the reservoirs of hydroelectric plants lack adequate structure for amphibian reproduction due to i) it's large size and lack of physical barriers, strong waves, making anuran activity and egg adherence to substrates difficult; ii) it's depth, leaving few suitable places for egg laying and tadpole development, which usually occur in shallow waters (Barreto & Moreira 1996) and iii) vegetation mortality at the edges, creating a strip of dead trees and exposed soil (Diamond 1972).

2.5 Climate change and future prospects

The large-scale agricultural conversion of the Cerrado has direct consequences for habitat availability and suitability as well as other indirect and less conspicuous effects. Simulations of the effects of converting natural Cerrado into open grasslands on regional climate have shown reduced precipitation, an increase in the frequency of dry periods within the wet season, changes in albedo and increased mean surface air temperature (Hoffmann and Jackson 2000).

The synergy between climate change and habitat loss is perhaps the greatest threat to biodiversity (Drake et al. 2005, Canhos et al. 2008). This becomes apparent when considering the projected scenario of habitat degradation for 2050. If human occupation of the Cerrado continues northward, as expected, the proportion of remaining natural habitats will be rapidly reduced, which will lead to a great loss of biodiversity (Diniz-Filho et al. 2009). In this case, only a small portion of suitable natural habitats will remain in northern Cerrado, with amphibian richness being reduced to less than half. As populations are already reduced in size by isolation due to habitat loss, increased temperature and reduced rainfall could lead to the extinction of populations and species (Bickford et al. 2010).

According to Silvano (2011), future climate will not be favorable to most Cerrado amphibians. Many species have restricted distributions, which increases the risks associated to climate change, since even relatively small changes may result in a reduction of their geographic distributions (Bush and Hooghiemstra 2005). In a realistic scenario, with a dispersal limit of 500 km around the biome, climate change should exert drastic effects on habitat suitability for amphibians. According to this author, most species will undergo more contraction than expansion of suitable areas in 2050. With an average of 30% range loss, many species would be threatened with extinction.

A species' ability to deal with disturbances and habitat fragmentation varies with its ecological and reproductive plasticity in the use of the altered habitats (Tocher et al. 2001, Brandão and Araújo 2001, Urbina-Cardona et al. 2006). The ability a species has to disperse will determine if they will occupy shifting suitable areas in the future or simply disappear as their habitats are destroyed. Therefore, because amphibians are highly dependent on dispersal corridors in highly anthropogenic environments (Gibbs 1998), it is important to assure the integrity of corridors or suitable areas to their dispersion (Araújo et al. 2006) between distant habitats. The forecasted climate changes can also impair species migration, especially considering the speed and magnitude of their occurrence (Araújo et al. 2006). Few amphibian species are able to disperse, within 50 years, across the 170 km. Therefore, displacement of suitable areas is an additional concern for Cerrado amphibian conservation, since southeastern Brazil is precisely the most disturbed and densely populated areas in Brazil (Marini et al. 2009). Likewise, the current and predicted areas of highest amphibian richness in the Cerrado coincide with densely populated areas with advanced degrees of degradation. Diniz-Filho et al. (2009) investigated the effects of climate change on patterns of vertebrate diversity in the Brazilian Cerrado and found that species distribution expansions may include areas already being used for livestock.

According to Pacífico (2011), future global climatic changes will have a strong negative effect on the anurans endemic to the Cerrado, especially those with small potential actual distribution. Anurans with small distributions will have to disperse in order to survive the alterations occurring on their native areas. Thus, the ability to disperse is paramount for the resilience of a species in a rapidly changing environment (Trakhtenbrot et al. 2005). However, besides the intrinsic ability every anuran species has to disperse, there are structural barriers (large rivers, mountains) and anthropogenic activities that

cause landscape fragmentation. This synergy exacerbates the negative effects generated by the global climatic changes, especially for small distribution species.

2.6 Conclusion

The world's largest and most diverse savanna is currently under major agronomic pressure. Despite the scarcity of studies regarding the effects of agricultural activities on native anurans, we were able to draw some conclusions from the main studies mentioned on this review (Table 2.1).

Commonly regarded as more resilient to disturbances than their forest counterparts, the anurofauna of the Cerrado is characterized by a series of life-history traits that may effectively render them more resistant to anthropogenic disturbances than Neotropical forest anurans. According to many studies, fossorial habits and specialized breeding structures such as foam nests might in fact be responsible for the resistance of some anurans in disturbed Cerrado habitats such as crops and pastures. However, much like what has been acknowledged in other biomes, these anthropogenic areas are dominated by widespread, generalist species. Hence, crops and pastures can harbor an anuran community, albeit strongly dominated by highly resilient species, favoring generalists and excluding specialists. Nonetheless, there is evidence that these generalist populations are in sub-optimal fitness conditions.

Maintaining natural vegetation fragments, earthen irrigation channels and shallow depressions that support perennial ponds and aquatic vegetation in order to maximize the potential of agroecosystems to harbor diverse anuran communities.

The anurofauna of the Cerrado is especially vulnerable to hydroelectric projects but the Brazilian government has been increasingly acknowledging the hydroelectric potential of the Cerrado, planning for the construction of more hydroelectric dams in a biome already largely converted into crops and pastures, putting the Cerrado's remaining biodiversity in a especially precarious position.

It is urgent to direct the attention to the Brazilian savanna. The scientific community must help establish the Cerrado as a valuable biome with major ecological importance. Detailed demographic and community-level studies on Cerrado amphibians are badly needed, namely abundance and species richness studies for adult, juveniles and

larvae/eggs. Furthermore, studies approaching species loss from a functional (Tilman 2001) and phylogenetic (Magurran 2005) point of view should be used as they allow a more thorough assessment of the effects on biodiversity, analyzing the changes in community composition. Invariably, as the Cerrado is transformed into the agricultural heart of Brazil, it is urgent to thoroughly assess the impacts on anuran communities, identify eventual threatened populations and develop efficient conservation policies in consonance with agricultural systems.

Table 2.1 Summary of the main studies approaching the effects of several anthropogenic activities on the anurans of the Cerrado.

Anthropogenic activity	Reference	Biome	Focus	Effect
Fire	Brasileiro (2004)	Cerrado	Community	• Species richness and abundance unaffected; • Higher interspecific competition for calling and egg-laying sites.
	Drummond (2009)	Cerrado	Community	• Increased species richness after the fire; • Increased abundance of the two endemic species of campos rupestres; • *Ischnocnema juipoca*, typical of fire-prone phytophysiognomies, was abundant throughout the area before the fire, but rarely found afterwards. • Higher frequency of terrestrial species with habits and breeding specializations (e.g. fossorial behaviors; foam nests) that render them more resilient to fire. • Negative effects on the arthropod-rich anuran diet. • Higher inter-specific competition for calling and egg-laying sites.
	Morais, Côrtes and Bastos (2011)	Cerrado	Community	• Co-occurrence patterns, anuran species composition and richness were unaffected by fire. • *H. albopunctatus* and *S. fuscomarginatus* were the most common species both in burned and unburned veredas. • *R. mirandaribeiroi* and *L. labirynthicus* were found exclusively in burned and unburned veredas, respectively.
Crops	Silva et al. (2009)	Cerrado	Community	• Only generalist terrestrial species were found in crops;

Anthropogenic activity	Reference	Biome	Focus	Effect
				• All species were represented by few individuals.
	Vaz-Silva (2009)	Cerrado	Community	• Waterbodies distant from monocultures show higher heterogeneity and species richness. • The Hylidae family is more represented in areas distant from crops. • Microhabitat availability was higher in waterbodies distant from crops. • Microhabitat use was higher in agricultural environments and most species encountered in both pristine and agricultural waterbodies had smaller niches in agricultural waterbodies.
	Morais (2011)	Cerrado	Community	• Species richness in waterbodies surrounded by large areas of crops was high and similar to what is estimated for protected areas in the biome; • Most of the recorded species were widespread, open area breeders and habitat generalists
	Duré et al. 2008	Northeastern Argentina	Community	• Anurofauna similar to that found in undisturbed wetlands • Natural vegetation supported the highest species richness • Pools with aquatic vegetation may explain the presence of frogs in rice fields and indicate the importance of such features for anuran populations.
	Machado and Maltchik 2010	Southern Brazil	Community	• 75% of the area's species richness found in rice fields; • species composition is different from pristine areas, dominance of hylids and leptodactylids • anuran richness and abundance changed over the rice cultivating cycle, peaking in the growing phases, during the warmer summer,

Anthropogenic activity	Reference	Biome	Focus	Effect
				with abundant surface water.
	Maltchik et al. 2011			• 60% of region's total species richness in rice fields, although dominated by species common in open areas. • tadpole abundance was low; higher number of tadpoles of species that deposit eggs in foam nests inside subterranean constructed chambers. hylid tadpoles in organic rice fields, which may be associated with the presence of a strip of vegetation close to these rice plots.
	Telles et al. 2007	Cerrado	*Physalaemus cuvieri*	• Human presence explains patterns of genetic distances in populations;
	De Marco et al. 2013	Cerrado	Community	• Amphibians are being positively affected by increased chlorophyll, ammonium, pH, and electric conductivity and negatively affected by increased transparency.
	Campos et al. 2013	Cerrado	Community	• Higher species richness and abundance in temporary lentic waterbodies; • Structural habitat heterogeneity favor more diverse communities in temporary ponds compared to lotic waterbodies and permanent lagoons. • Lentic temporary waterbodies harbored many species, but all are generalists, associated to anthropogenic environments.
Agrochemicals & Diseases	Simioni, Silva and Mott (2013)	Cerrado	*P. albonotatus*	• CL_{50} for *Physalaemus albonotatus* was four times smaller than the value found for a congeneric species (*P. centralis*) using the same protocol.

Anthropogenic activity	Reference	Biome	Focus	Effect
	Figueiredo and Rodrigues (2010)	Cerrado	*P. centralis, R. marina, Elachistocleis sp.*	• Higher values of CL_{50} for *Rhinella marina* and *Elachistocleis* sp.
	Moreira et al. (2012)	Cerrado	*Rhinella schneideri Leptodactylus labyrinthicus.*	• Endosulfan residues were detected in the blood plasma of *R. schneideri* and *L. labyrinthicus.*
	Lima (2010)	Cerrado	*L. ocellatus*	• Liver and skin showed histopathologic changes, but the liver was especially damaged in animals from both pristine and agricultural areas.
	Ramalho (2015)	Cerrado	Community	• Thirteen species extant in the Cerrado have been found infected by *Bd* • Confirmed *Bd* on endemic *Bokermannohyla pseudopseudis* species group, typical from small high altitudes, with stream-dwelling tadpoles.
Hydroelectric exploration	Brandão & Araújo 2008	Cerrado	Community	• After complete flooding, only 11 of the 31 species originally found were still recorded on the site. • Previously common, widespread and generalist species suffered severe declines or went extinct following complete flooding. • Only *R. schneideri* used the lake for reproduction.
Pastures	Silva, Candeira and Rossa-Feres (2011)	Cerrado	Community	• Anuran species richness in farmland ponds is mainly predicted by marginal vegetation height and other variables related to habitat heterogeneity that reflect the structural complexity of breeding

Anthropogenic activity	Reference	Biome	Focus	Effect
				sites.
	Silva et al. (2011)	Cerrado	Community	• Generalist species used both pasture and forest habitats and were forced to cross open habitats to reach the breeding sites. • Ponds at the forest fragment-matrix transition had higher anuran abundance and species richness than those far from or within forest fragments.
	Silva et al. (2012)	Cerrado	Community	• Breeding areas located at the edge or close to forest fragments support greater anuran richness and abundance than more isolated breeding areas
	Silva and Rossa-Feres (2011)	Cerrado	Community	• Dominant species were the same in pools close and distant from forest fragments. Species were more abundant in pools close to forest fragments. • Many species showed prolonged breeding activity (i.e. calling) in pools closer to forest fragments.
Climate change	Hoffmann and Jackson 2000	Cerrado	Biome	• Converting natural Cerrado into open grasslands on regional climate have shown reduced precipitation, an increase in the frequency of dry periods within the wet season, changes in albedo and increased mean surface air temperature.
	Diniz-Filho et al. 2009			• Occupation of the Cerrado will continue northward, the proportion of remaining natural habitats will be rapidly reduced, which will lead to a great loss of biodiversity (Diniz-Filho et al. 2009). • Only a small portion of suitable natural habitats will remain in northern Cerrado, with amphibian richness being reduced to less than half.

Anthropogenic activity	Reference	Biome	Focus	Effect
	Silvano 2011			• According to this author, most species will undergo more contraction than expansion of suitable areas in 2050. With an average of 30% range loss, many species would be threatened with extinction.
	Pacífico 2011			• Future global climatic changes will have a strong negative effect on the anurans endemic to the Cerrado, especially those with small potential actual distribution.

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"Aprendo mais com abelhas do que com aeroplanos.
É um olhar para baixo que eu nasci tendo.
É um olhar para o ser menor, para o
Insignificante que eu me criei tendo.
O ser que na sociedade é chutado como uma
barata – cresce de importância para o meu
olho.
Ainda não entendi porque herdei esse olhar
para baixo.
Sempre imagino que venha de ancestralidades
machucadas.
Fui criado no mato e aprendi a gostar das
coisinhas do chão –
Antes que das coisas celestiais
Pessoas pertencidas de abandono me comovem:
Tanto quanto as soberbas coisas ínfimas."

Manoel de Barros, *Retrato do artista quando coisa.*

Chapter 3

An integrated trait-based framework to predict extinction risk and guide conservation planning in biodiversity hotspots

3. AN INTEGRATED TRAIT-BASED FRAMEWORK TO PREDICT EXTINCTION RISK AND GUIDE CONSERVATION PLANNING IN BIODIVERSITY HOTSPOTS

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3.1. Abstract

Determining species extinction risk and its drivers is a major goal for conservation biology. The IUCN Red List is widely used for classifying extinction-risk and prioritizing conservation action. However, this system has been acknowledged as biased and complementary approaches are strongly recommended to achieve more reliable conclusions on conservation priorities. Species traits, often perceived as determinant for resiliency to disturbances, have been used to identify potentially vulnerable species, even when data are scarce (e.g. Data Deficient species). We provide an integrative and cost-effective framework for predicting species extinction-risk using data on 195 anurans from the Cerrado. We used IUCN population trend and expert-perceived vulnerability to habitat alteration as response variables, to identify traits associated to increased extinction-risk. We used species traits, threat pressure and geographic range to determine which species and areas had higher conservation priority. We found the official extinction-risk to be underestimated, as many species categorized as LC or DD are actually sensitive and/or declining. We identified breeding site, habitat and clutch size as predictors of anuran extinction risk. We found that >70% of the biome's anurans have major protection gaps, incurring in high extinction-risk. The southwest and central region of the biome are the main hotspots for high extinction-risk

species and should be prioritized for conservation. Our framework may be particularly valuable to assess extinction-risk and prioritize conservation action regarding less studied taxa and regions with high anthropogenic pressure, but weak government support and scarce funding.

Key Words: Cerrado, amphibians, Neotropics, Red List.

3.2. Introduction

Vulnerability to disturbance differs across species and many systems have been devised to determine extinction risk, aid in conservation planning and raise public awareness. The most prevalent of these systems is the IUCN Red List of Threatened Species (henceforth "Red List"), developed by the Species Survival Commission of the World Conservation Union (IUCN; http://www.iucn.org). The Red List highlights species at greater risk of extinction, aiming to prioritize conservation action. The Red List classifies species based on quantitative data on population size and geographic range (IUCN, 2001). If population size or range have been shown to decline, species are classified as threatened (Critically Endangered (CR), Endangered (EN) or Vulnerable (VU)). If threat criteria are not met, species are classified as not threatened (Near Threatened (NT), Least Concern (LC)) or, when there is no sufficient data for categorization, as Data Deficient (DD). The Red List has been paramount for establishing protection priorities and justifying conservation funding (Baillie et al., 2008; Mace and Baillie, 2007; Young et al., 2014). However, conservation status is more relative than absolute, in the sense that a classification of CR does not imply that the species is almost extinct, but only that it is in greater danger of becoming extinct - even if by stochastic events - compared to a species that is classified in any other category.

The Red List's reliability stems from its criteria, which are objective and relatively easy to apply when adequate information is available (IUCN, 2001). These criteria were, however, defined based on the requirements of large vertebrate species, causing the system to be putatively biased towards larger and easily sampled taxa (Cardoso et al., 2011; Régnier et al., 2015; Triantis et al., 2010). Hence, even if enough information could be gathered, they may not be appropriate for many taxa. Furthermore, decade-long re-evaluation periods may render the Red List unable to detect shifts in extinction-risk for fast-declining species, further compromising its effectiveness. Despite its unarguable value for conservation, the Red List should not be used as the sole means of setting priorities for conservation measures (IUCN, 2001). This recommendation is rarely appreciated and, due to the system's importance in current conservation circles, its bias is often pervasive in species inventories (Cardoso et al., 2011), reintroduction projects (Seddon et al., 2007), invasive species studies (Pyšek et al., 2008), legally protected species lists and conservation funding (Cardoso et al., 2011).

Although there is a considerable degree of classification consistency, the Red List does not take into account species life histories, causing under- or over-estimated extinction-risks in certain cases (IUCN, 2001). Hence, threat category provides only a relative assessment of the extinction-risk under current circumstances, and should not be used in isolation. A system for assessing priorities for action should include numerous other factors concerning conservation action, such as biological characteristics of the subject, costs, logistics and chances of success (IUCN, 2001).

Our understanding of which species are most at risk remains poor, especially for inconspicuous taxa, for which natural histories have not been well documented and population changes are hard to detect (Cardoso et al., 2011). For example, according to the Red List, 32.4 % of the world's amphibians are threatened or extinct, and 24.4% are unclassified (DD), due to insufficient information (IUCN, 2008). Amphibians are among the least studied vertebrates when compared to birds and mammals (Hecnar, 2009), due to their inconspicuous nature and small size (Wells, 2007). In a highly anthropogenic world, with alarming climate change predictions and limited funding for conservation, it is vital to develop more accurate and case-specific frameworks to prioritize conservation actions and aid mitigation.

Differences in species extinction risk have been partially attributed to variation in biological traits (Pearson et al., 2014; Van Allen et al., 2012). Indeed, habitat preferences, ecological traits and demographic characteristics have been successfully used to predict species' extinction risk (e.g. Cardillo et al., 2005; Davies et al., 2004; Lee and Jetz, 2011; Pearson et al., 2014). Therefore, understanding how species traits interact to determine extinction-risk may help identify species at greater risk and prompt cost-effective and timely conservation measures.

Amphibians play keystone roles in ecosystem functioning, acting as both predators and prey, and enabling nutrient transport between aquatic and terrestrial systems (Blaustein et al., 2011; Wells, 2007). Furthermore, amphibians are among the most diverse and abundant vertebrates, comprising species from a variety of habits, breeding strategies and dispersal abilities (Wells, 2007). Due to their biphasic life cycle, highly permeable skin and ectothermic physiology, amphibians are very dependent on environmental quality and vulnerable to its change (Niemi and McDonald, 2004). Hence, amphibian extinction risk can be used as a

surrogate for ecosystem resilience (Davic and Welsh, 2004) and a suitable model for conceiving a new framework to informatively predict extinction risk.

The Cerrado is the world's largest and most biodiverse savanna. It is also Brazil's new agricultural frontier, hosting the country's largest bovine herd and a percentage of crop area larger than that of the Amazon. About 40% of the biome has been converted into crops and pastures (Sano et al., 2010) and only 6.48% is under protection (Arruda et al., 2008; Overbeck et al., 2015). The anuran assemblage of this biome has high endemicity (*ca*. 50%) (Valdujo et al., 2012), but low official extinction risk, as only 3 amphibians are considered threatened (IUCN, 2014, MMA, 2014), while 22% remain Data Deficient. Discrepancy between low extinction risk, high endemicity (Valdujo et al., 2012) and intense anthropogenic pressure may be explained by historical biases towards Neotropical forest biomes, such as the Amazon or the Atlantic Forest. For example, sixteen Atlantic Forest anurans are threatened, but a Web of Science (apps.webofknowledge.com, accessed on April 2015) search using ''Atlantic Forest'' or ''Cerrado'' in combination with "amphibians" retrieved 3 times more journal articles on the Atlantic Forest than on the Cerrado.

With the ever-increasing anthropogenic pressure on biomes worldwide, many species may be unrecognizably endangered. There is a need for integrative, predictive and spatially explicit models capable of accurately identifying species at higher risk, evaluating the consequences of disturbances for biodiversity and guiding conservation actions, especially in biodiverse, highly disturbed and scarcely studied regions. Herein we assess amphibian extinction risk and identify its drivers in a highly disturbed biodiversity hotspot. We propose an integrative and cost-effective method for accurately assessing and predicting extinction risk, considering species rarity, threat pressure and trait-based vulnerability to disturbances. We compiled an extensive database with 12 biological traits (e.g., activity, habits) and 4 variables describing threat pressure (e.g., percentage of a species' range occupied by crops) for 195 Cerrado anurans. First, to identify traits associated to increased extinction risk across species, we used two proxies for extinction risk as response variables: IUCN population trend and expert-perceived vulnerability to habitat alteration. This analysis allowed us then to (i) predict population decline and vulnerability to habitat alteration for every species; (ii) use our results to calculate integrative species-specific conservation targets; (iii) perform a gap

analysis to evaluate how effective the network of the biome's protected areas (PA) is, and which are the species with more urgent conservation needs, and (iv) build maps representing areas with increased extinction-risk.

3.3. **Methods**

3.3.1. Data collection

We compiled intrinsic biological traits and extrinsic environmental variables for 195 species of anurans extant in the Brazilian Cerrado. We used the species list from Valdujo et al. (2012) and crossed it with the IUCN distribution maps (IUCN, 2008). This data crossing motivated us to exclude species for which we could not find satisfactory distribution maps, and include others not considered by Valdujo et al. (2012), with mapped occurrence in the Cerrado. The biological traits we considered for this study were anuran activity, adult snout-vent length (SVL), geographic range size, habitat, habit, fossorial behavior, breeding site, breeding strategy, clutch size, parental care, breeding season and breeding pattern. We also considered 4 variables quantifying extrinsic environmental variables, namely the percentage of range area in Cerrado, and percentage of natural vegetation, crops and pastures within each species' geographic range in the Cerrado (Table A1, Supplementary material). Trait data were compiled from the literature, AmphibiaWeb and IUCN online databases. If published data were unavailable, we relied on expert opinion. External threats were quantified using species distribution maps (IUCN, 2008) and a shapefile of land use in the Cerrado (e.g., agriculture, urban areas) provided by the Brazilian Ministry of Environment (MMA, 2007). We determined the percentage of each species' range occupied by crops, pastures and natural vegetation using program QGIS v.2.6.1 Brighton. Predictor variables were chosen based on our perception of their importance for determining species responses to anthropogenic disturbances, and also on data availability.

To identify which traits are associated with increased extinction risk across species, we used two proxies for extinction risk obtained from the IUCN Red List online database, as response variables. Due to the relatively low percentage of threatened amphibians (CR, VU, EN) among the 195 known from the Cerrado, we used other two variables provided by IUCN: (i) population trend, and (ii) expert-perceived vulnerability to habitat alteration. Both

population trend and expert-perceived vulnerability were obtained from each species' fact sheet on the IUCN Red List database. This information is based on empirical data collected by experts. Population trend is categorized as declining (D), stable (S), increasing (I) or unknown (U). According to this variable, 13% of the species have declining populations, 58% have stable populations and 26% have unknown population trends. Expert-perceived species vulnerability to habitat alteration was gathered from uncategorized information given by experts based on their empirical field experience on how often a species is found in disturbed areas. We considered a species either tolerant to habitat alteration (T) if it is commonly found in disturbed areas, sensitive (S) if it tends to disappear after disturbances, or unknown (U). The IUCN online database has information on each species' vulnerability to habitat alteration for most cases. When this was omitted we searched the literature and, if necessary, contacted the species assessor(s) credited on the factsheet. We contacted over 20 experts for clarifying both trait and vulnerability uncertainties. Experts contacted were based on institutions ranging from the states of Bahia, to Goiás and São Paulo. Only when we could not get information from any of these sources, we would classify species vulnerability to habitat alteration as unknown. According to this variable, 23% of the anurans occurring in the Cerrado are sensitive to habitat alteration, whereas 46% are considered tolerant and 30% of the species have unknown sensitivity to habitat alteration.

3.3.2. Data analysis

Machine learning techniques are a powerful alternative to traditional linear models and have documented advantages for extinction risk analyses, especially when the goal is predictive accuracy (Davidson et al., 2009; Murray et al., 2011). Classification-tree models identify nonlinear, context-dependent associations among multiple correlated predictor variables (Olden et al., 2008). These methods do not assume a specific distribution of predictor variables or data independence, avoiding concerns about pseudoreplication and alleviating the need for phylogenetic control (Bielby et al., 2009).

To identify which traits and/or external threats were associated with increased extinction risk measured by (i) population trend and (ii) expert-perceived vulnerability to habitat alteration, we used random forest models. This approach combines the predictions of

many independent decision-tree models to produce a robust classification (Breiman, 2001), determine predictor importance and predict vulnerability and population trend for each species, especially those for which information is unknown. However, because random forest models cannot graphically represent how each trait influences population decline and species vulnerability, we also used traditional decision-tree models for that purpose.

We assessed model accuracy through the percentage of species correctly classified (PCC), the percentage of species not threatened that are correctly classified (specificity), the percentage of threatened species that are correctly classified (sensitivity), and Cohen's kappa, which measures inter-rater agreement for qualitative items between two classifications. Cohen's kappa is considered more robust than percent agreement calculations, since it accounts for the agreement occurring by chance. We calculated Cohen's kappa statistics for agreement and further tested the null-hypothesis that the extent of agreement is random (kappa statistic equals zero) using package irr (Gamer, 2015) on program R v.3.1.2 (R Core Team 2014). We built random forest and classification-tree models using packages randomForest (Liaw and Wiener, 2015) and rpart (Therneau and Atkinson, 2012) also on program R. Classification trees are built by repeatedly partitioning the dataset into a nested series of mutually exclusive groups, each group as homogenous as possible regarding the response variable, according to the mean decrease in accuracy (Liaw and Wiener, 2015). Branches are afterwards pruned by 10-fold cross-validation to produce an "optimal tree", balancing complexity (i.e., number of nodes) with prediction accuracy. The smallest tree with an error rate within 1 standard error of the minimum-error tree is taken as the most parsimonious tree, the "optimal tree".

Although decision-tree models do not assume data points to be independent, alleviating the need to "correct" for phylogenetic relationships between species, we used a taxonomic variable (family) to evaluate the role of taxonomy in population trend and expert-perceived vulnerability.

To visualize how vulnerability to habitat alteration and population trend is geographically distributed, we created heatmaps of high extinction risk zones by overlapping geographic ranges of anuran species with traits identified as vulnerability- or decreasing-prone by our models using program QGIS v.2.6.1 Brighton.

To evaluate the conservation efficiency of the Cerrado PA network, we performed a gap analysis. Gap analysis is a version of the well-established method of identifying gaps in the representation of biodiversity in management areas (Scott et al., 1993). Digital map overlays are used in GIS environment to identify individual species, species-rich areas, and vegetation types that are underrepresented (Scott et al., 1993). Gap analysis is considered one of the most successful tools for detecting whether a PA system adequately protects a given species or assemblage, requiring: (i) an estimate of its distribution in the region, (ii) the identification of protected sites, and (iii) the definition of explicit conservation targets necessary to ensure acceptably small extinction risks (Pressey et al., 2003). Conservation targets represent the minimum amount of a particular biodiversity feature (e.g., habitat type) that should be conserved through conservation actions (Carwardine et al., 2009). The most commonly used targets in conservation are equivalent for all species (Urbina-Cardona and Flores-Villela, 2010) or for groups of species with equivalent distributions (Catullo et al., 2008; Marini et al., 2009). These can favor widespread species (Vimal et al., 2011), failing to acknowledge that some may require more extensive protection than others (Pressey et al., 2003). We adopted a specific approach based on (i) species' geographic range, resulting in larger targets for species with smaller distributions, and recognizing the increased risks that extensive impacts present for unprotected portions of their distributions (Pressey et al., 2003); (ii) susceptibility, accounting for the percentage of habitat loss and an estimate of extinction threat, represented by species population trend and vulnerability previously predicted, and (iii) life-history, accounting for life-history traits previously identified as determinant for decreasing population trend or increased vulnerability: breeding site; habitat; clutch size and body size.

Geographic range (*GR*), susceptibility (*SU*) and life-history (*LH*) components were calculated as shown in de Novaes e Silva et al. (2014). Species sensitive to habitat alteration are expected to have increased need for protection, to avoid high exposure to disturbances. Hence, we ranked the *SU* component as 1 for sensitive, 0.1 for tolerant, or 1 for decreasing and 0.1 for stable. This ensured that susceptible species were attributed higher conservation targets. For the *LH* component, accounting for life-history (biological traits), we used the outputs from our random forest and classification trees models to assign values and relative

importance to each trait and respective attribute. To input trait importance for extinction-risk and, therefore, conservation target, we used the mean accuracy decrease value. This represents the relative importance of each predictor for vulnerability and population trend, measured by the reduction in classification accuracy upon removal of each trait in a set of 2000 random forest trees. To input trait attribute importance, we used the results form our classification tree model to define which attribute was more associated to increased extinction-risk. For example, for breeding site we used 22.5 to input trait relative importance, and attributed different values according to association to lotic (1) or lentic (0.3) breeding sites, as association to lotic environments was a predictor of increased vulnerability in our classification tree models. This way, a species with lotic breeding habits will have increased conservation targets compared to a pond breeding species, due to our predictions of increased extinction risk for the previous. The other three more important traits were accordingly classified, and the values summed to describe species sensitivity due to life-history traits.

To calculate conservation targets, we weighted the *GR* component twice as much as the other two criteria, to avoid putting too much emphasis on the conservation of widespread species and also recognizing the prominent role of range size in determining the risk of extinction (Harnik et al., 2012). We tuned the formula so that a minimum theoretical value of about 10% of every species' pristine range was guaranteed, a value that has been widely used as a uniform target (de Novaes e Silva et al., 2014; Pressey et al., 2003). We calculated the conservation target for each species *i* as:

$$T_i = 0.065 + 0.1GR_i + 0.05SU_i + 0.05LH_i,$$

where *GR* is geographic range, *SU* is susceptibility (population trend/vulnerability), and *LH* is sensitivity due to life-history traits.

We conducted a global sensitivity analysis to determine the influence of uncertainty in model input upon the uncertainty in model output (Saltelli, 2002), generating 10,000 samples from the 3-dimensional parameter space (*GR, SU, LH*) using the Latin Hypercube Sampling and assuming a uniform distribution for each parameter, with package pse (Chalom and Prado, 2014) on program R. Using maps of the Cerrado's PA network (MMA, 2007), we also

quantified the percentage of target area currently under protection for each species, considering species with ≥ 50% of the target achieved as minor gaps and those with < 50% of the target achieved as major gaps.

Our framework is composed of 3 steps, initially requiring (i) proxies for extinction-risk obtained mostly from the IUCN online database, (ii) data on 12 biological traits, (iii) distribution maps for every species and (iv) quantification of threat pressure on each species' range. In a second step, we analyze this data using random forest and classification tree models, to (i) identify traits associated to increased extinction-risk and (ii) predict population trend and vulnerability to habitat alteration for every species, including species for which there is no information on those parameters. In the final step of the framework, we use (i) the traits associated to increased extinction risk, (ii) species' geographic range and (iii) predicted susceptibility (population trend and vulnerability) to calculate conservation targets and identify high priority species and areas (Fig. 3.1).

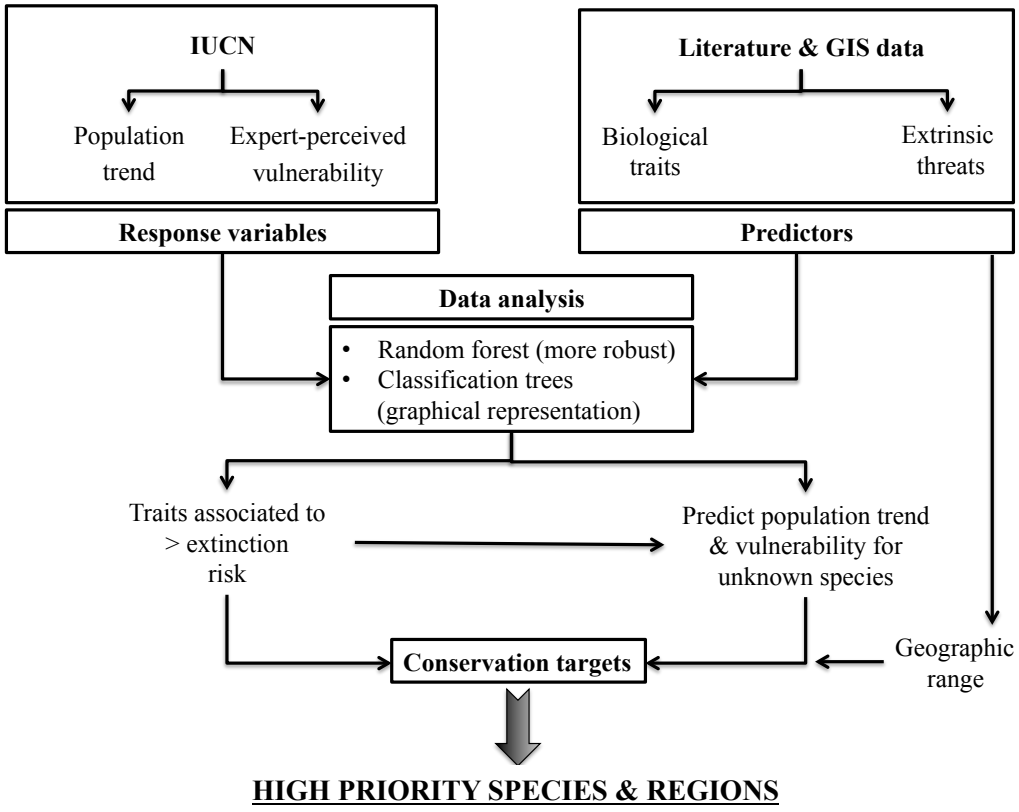

Figure 3.1. Schematic representation of the presented framework.

3.4. Results

Classification accuracy of the random forest model was high (PCC = 77%, Cohen's kappa = 0.32, $p = 0.001$). Breeding site was the most important predictor of vulnerability (Fig. 3.2), though total geographic range, % Cerrado range, habitat, clutch size, breeding strategy and SVL were also important (Fig. 3.3). The optimal classification tree predicted amphibian vulnerability with 79% accuracy (PCC, Cohen's kappa = 0.54, $p < 0.001$). Regarding population trends, classification accuracy of the random forest model was high (PCC 83.3%, Cohen's kappa = 0.34, $p < 0.001$) and similar to the optimal classification-tree model. Because the difference between the two most parsimonious trees was very small, we choose two classification trees for graphical representation, the "optimal classification tree" and the "second-optimal classification tree" for graphical representation. Despite high model

accuracy, sensitivities of both classification tree and random forest models were low (27% and 11.5%, respectively), indicating a low model ability to predict species with declining populations, due to high unbalance in the proportion of species with declining (8%) or stable populations (92%) (Fig. 3.4A).

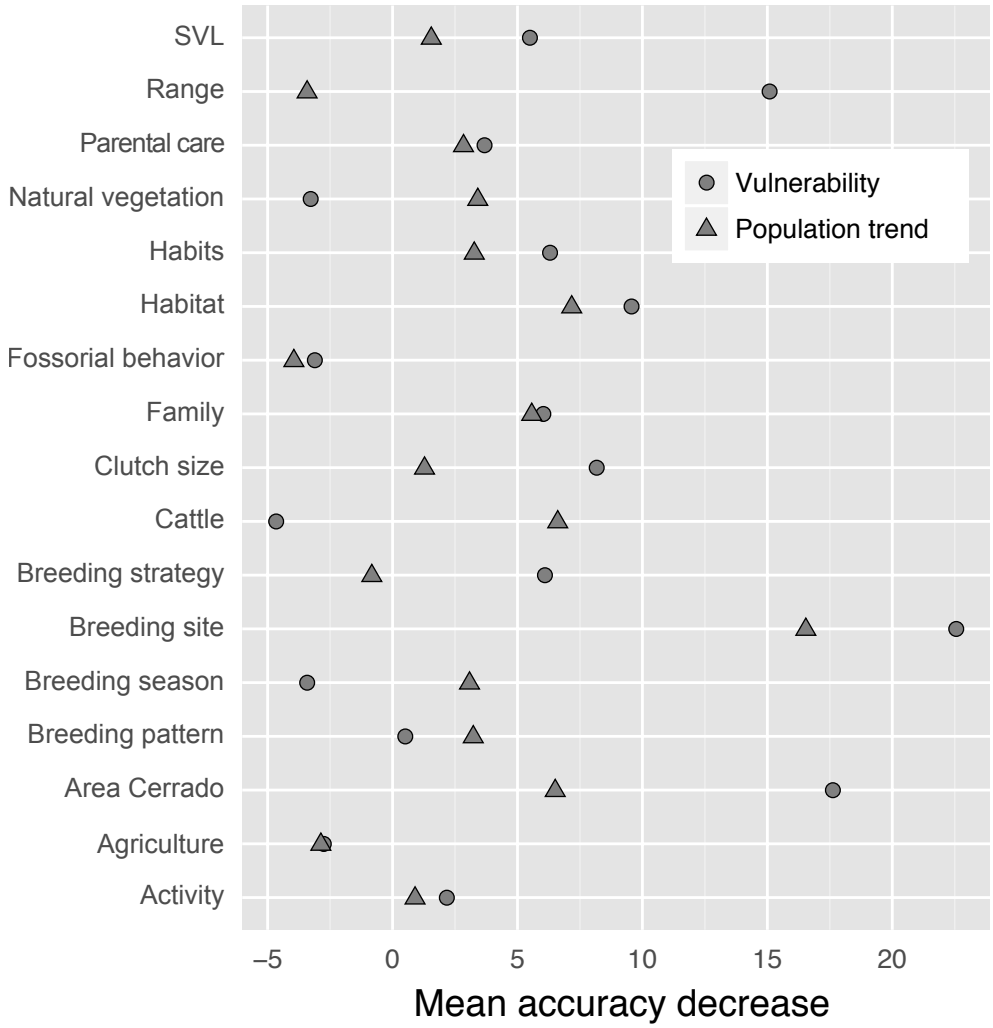

Figure 3.2. Relative importance of biological traits and external threats used as independent variables in random forest models using (i) population trend (triangles) and (ii) amphibian vulnerability to habitat alteration (circles) as response variables. Predictor importance is measured by the reduction in classification accuracy upon a stepwise removal of each trait in a set of 2000 random forest trees.

Our classification trees allow us to visualize the importance of each trait and respective attributes in determining species vulnerability and population trend. Regarding vulnerability, the first major split in the optimal tree separates anurans that have stream-associated breeding strategies from the rest, mostly pond breeders (Fig. 3.3).

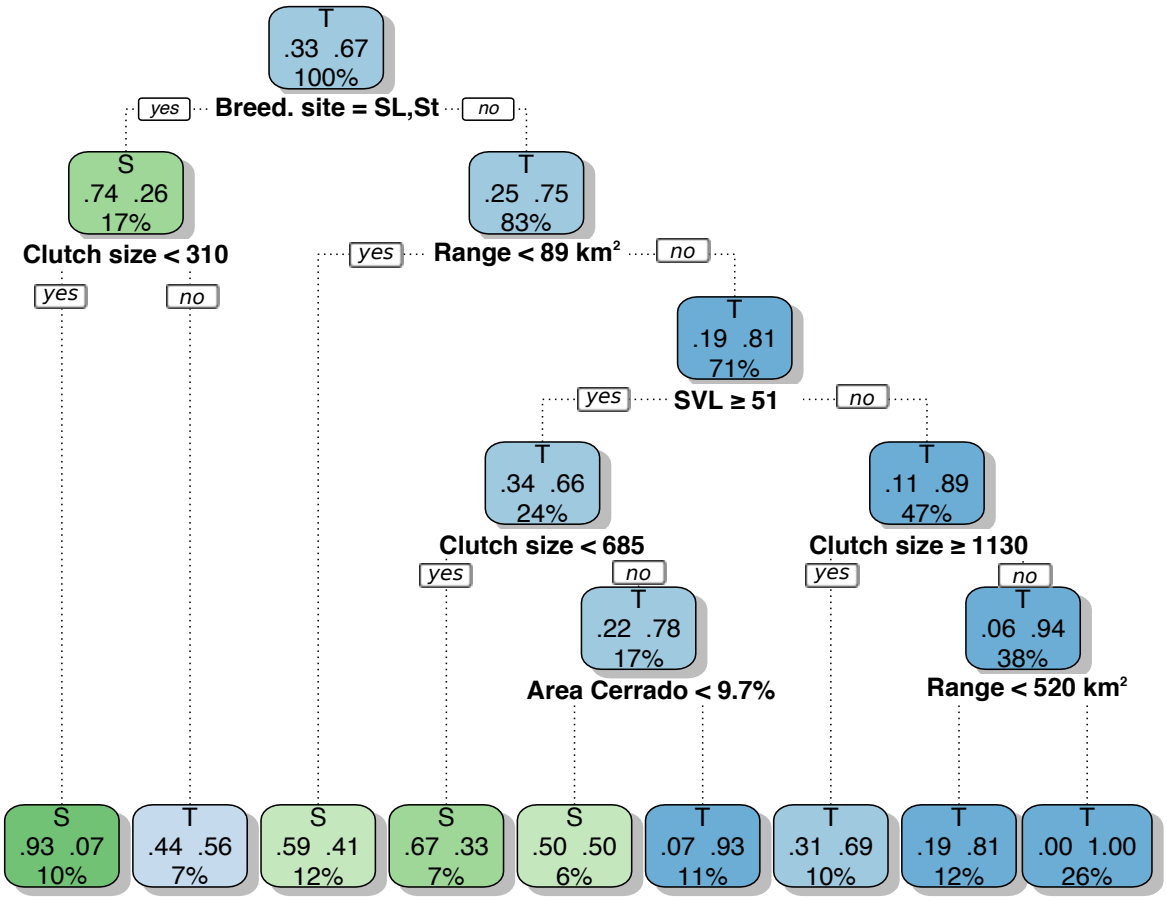

Figure 3.3. Classification tree showing anuran vulnerability according to external threats and intrinsic biological features. First set of values in each box describes the proportion of species sensitive and tolerant in that split and the percentage refers to the proportion of total species inserted in that split. Sensitive species are depicted in green shades, whereas tolerant species are depicted in blue shades. Shades vary according to the proportion of species in the group considered tolerant or sensitive, i.e. larger proportions are represented in darker shades. SL= Land & lotic water bodies (species that lay the clutch in terrestrial environments. such as the leaf-litter but transport the larvae to streams.); St = Lotic water bodies (species that breed in lotic water bodies such as streams).

However, not all stream-breeding species are highly vulnerable; stream-breeding species with large clutches (> 310 eggs) have 56% probability of being tolerant to habitat degradation. Fifty-nine percent of species with smaller geographic ranges have higher probabilities of being

sensitive to habitat alteration, but 67% of the anurans with broader ranges, larger than 51 mm SVL and with clutches smaller than 685 eggs are also vulnerable to habitat alteration.

Breeding site was the best predictor of population trends (Fig. 3.2), although habitat, % of pasture area inside the geographic range and range in the Cerrado were also important. The "optimal" decision tree indicated that only taxonomic family predicted population trend, although the "second-optimal" decision tree indicated that breeding site and habitat predicted population trends (Fig. 3.4). Seventy percent of anurans belonging to Brachycephalidae, Centrolenidae, Ceratophryidae, Craugastoridae and Hylodidae have decreasing populations (Fig. 3.4A). Breeding site is also important for predicting decreasing population trends; 52% of stream-breeding species have decreasing populations (Fig. 3.4B). This model indicates that habitat acts along with breeding site, resulting in 73% of the stream-breeding species from forests or rupestrian fields having decreasing populations.

About 41% of the species considered sensitive to habitat modification according to the information gathered from the IUCN Red List online database are considered DD by IUCN, 55% LC and only 3.6% are considered threatened (EN, VU or CR) (Table 1). About 77% of the species with verified decreasing population trends are considered LC, 11% as DD and 7.7% as threatened. The fact that most species considered decreasing are currently categorized as LC, suggests that the Red List may indeed be underestimating the extinction risk of the Cerrado anurans. We compared vulnerability gathered from the Red List online database to the vulnerability predicted by our model and found original and predicted vulnerability to be similar regarding distribution along Red List statuses. About 41% of decreasing species are listed as DD, 53% as LC and only 5.8% as threatened (Table 1). Considering every species listed as DD, 65% are predicted as sensitive, 11% as decreasing and 17% as sensitive and decreasing (Table A2, Supplementary material).

According to our heatmaps, anurans sensitive to habitat alteration appear more densely concentrated in the center of the Cerrado, and in other smaller and more isolated areas in the southwestern region (Fig. 3.5A). Likewise, decreasing species are also concentrated in the center of the Cerrado (Fig. 3.5B).

The global sensitivity analysis revealed a null expectation of 21.7 ± 2.3% for the conservation target (T_i). As such, and considering the range of observed values, only those

species with T_i larger than 25.5, deviated significantly from the null expectation (Z-test, $p < 0.05$) (Table A3, Supplementary material). These species are experiencing a higher extinction risk than expected by chance, given the model constraints. According to our conservation targets, 141 anuran species currently are major conservation gaps, i.e., the percentage of the species range under protection corresponds to less than 50% of its conservation targets, while only 29 species are protected.

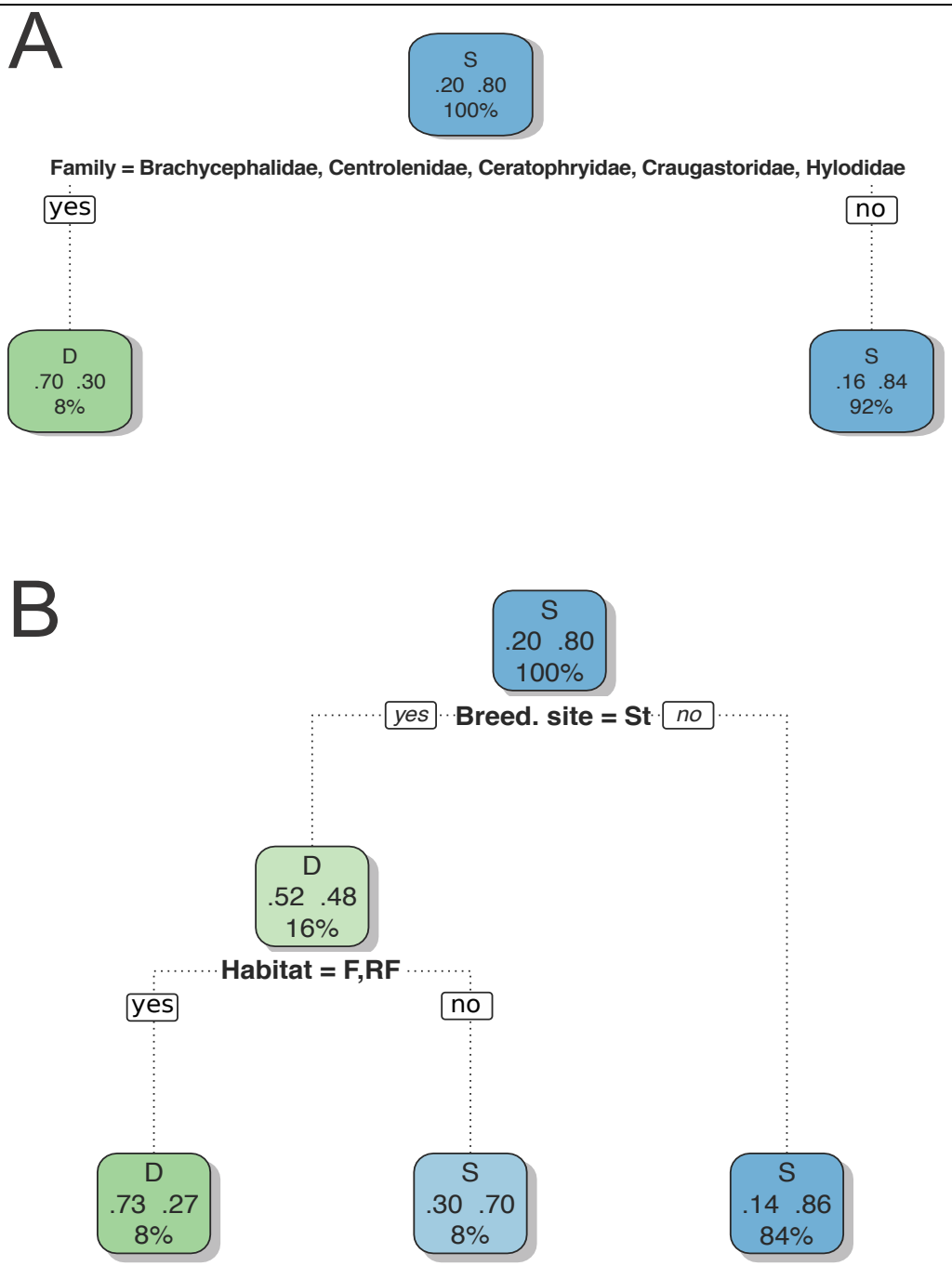

Figure 3.4. Classification tree showing anuran population trend according to external threats and intrinsic biological features. A) Optimal classification tree (most parsimonious model); B) Second optimal classification tree (second-most parsimonious model). First set of values in each box describes the proportion of species decreasing and stable in that split and the percentage refers to the proportion of total species inserted in that split. Decreasing species are depicted in green shades, whereas stable species are depicted in blue shades. Shades vary according to the proportion of species in the group considered decreasing or stable, i.e. larger proportions are represented in darker shades. St = Stream; F = Forest; RF = Rupestrian fields.

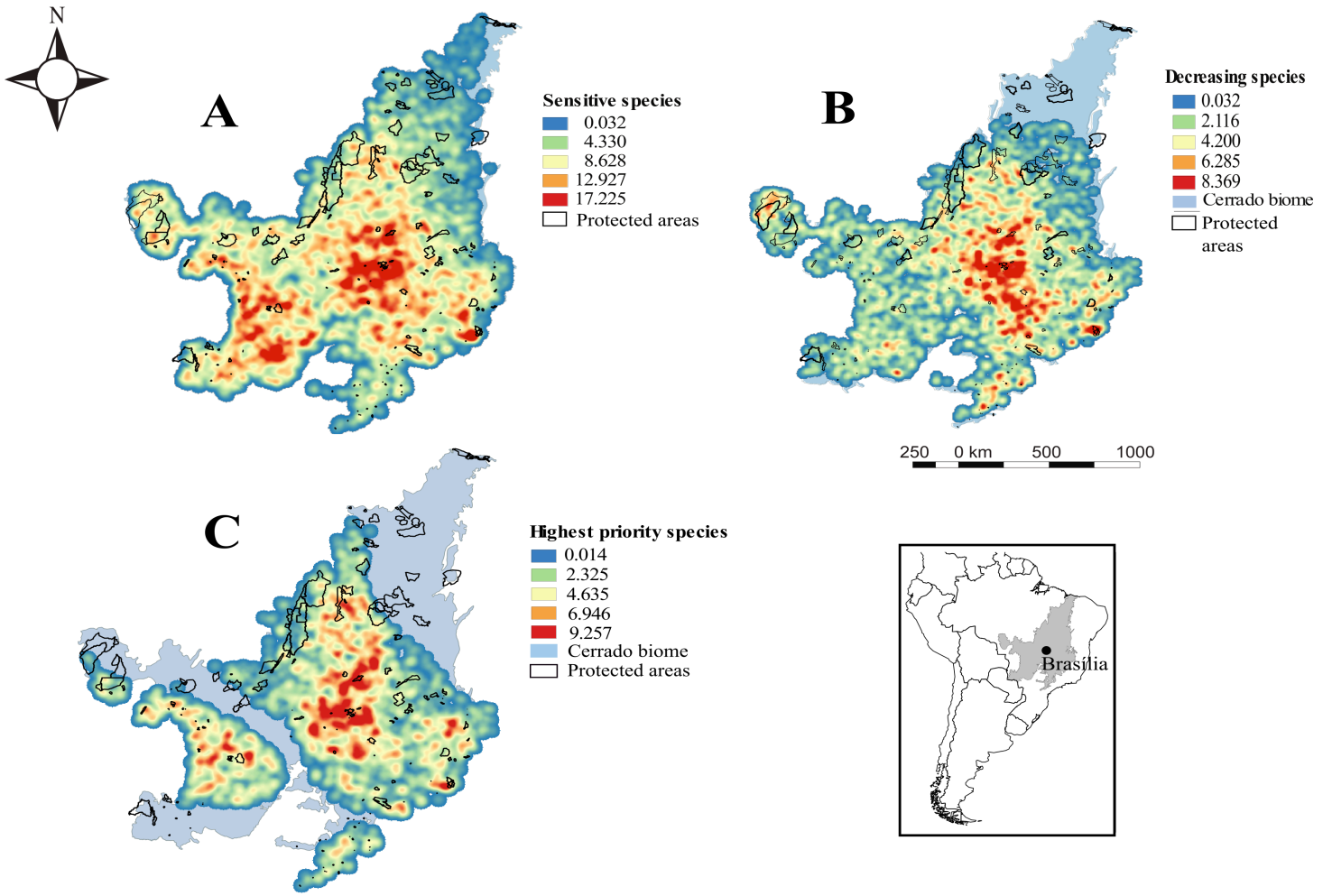

Figure 3.5. Geographical representation of density (mean number of species per area) for A) sensitive species, B) decreasing species C) highest priority species with increased conservation needs, i.e. species with a significantly higher than expected conservation target and a percentage of target achieved lower than 10%. Vulnerability and population trend heatmaps were built according to the predictions of our random forest models. Due to the lower sensitivity of our population trend model, we used species originally considered as declining along with species predicted as declining by our models but with originally unknown population trend to build the declining populations heatmaps

3.5. Discussion

Our study demonstrates that the most vulnerable anurans in the Brazilian Cerrado are a highly non-random subset of the assemblage regarding certain biological traits. Using two proxies for extinction risk (population trend and expert-perceived vulnerability), we were able to identify lotic breeders and habitat specialists with small clutches, large body sizes and small geographic ranges as those associated with increased risk of extinction.

The traits we found associated with increased extinction risk corroborate several other studies regarding a wide array of taxa (Murray et al., 2011; Olden et al., 2007; Siliceo and Díaz, 2010; Sodhi et al., 2008; Tomiya, 2013). Compared to generalists, specialists are considered less capable of dealing with new environmental challenges (e.g., habitat loss, climate change) because they are often unable to persist outside of their narrow range of preferred conditions (Murray et al., 2011). Lotic breeding habits, habitat specialization, small clutches, large body size and small geographic range have all been acknowledged as surrogates for higher degrees of specialization on multiple taxa (Prado and Haddad, 2005; Sagot and Chaverri, 2015; Siliceo and Díaz, 2010; Wells, 2007). Stream-breeding species appear particularly sensitive to habitat alteration, which is not a new finding. Stream-dwelling larvae are highly specialized in microhabitat use for foraging and cover. Specialization can render species susceptible to even minor environmental changes altering their ability to seek cover or forage (Welsh and Ollivier, 1998). We found that stream-breeding species with small clutches are especially sensitive to habitat alteration, which has not been previously reported. Cooper et al. (2008) found that clutch size is a significant component of geographical range size, while Hero et al. (2005) suggested that more fecund species might have greater potential to spread to new areas and occupy large geographical ranges. If larger clutches are related to larger ranges, higher dispersal ability and colonization success in amphibians, smaller clutches may render species more susceptible to stochastic events and anthropogenic activities, resulting in increased sensitivity to habitat alteration (Grafe et al., 2004; Pounds et al., 2006).

Range size was a predictor of species vulnerability to habitat alteration, especially for pond breeders. These results corroborate previous findings that small geographical range correlates with population decline or extinction risk in frogs (Botts et al., 2013; Sodhi et al.,

2008). Anurans with small ranges may be more vulnerable than those with larger ranges because they are at greater risk from activities affecting their entire range. For example, several endemic amphibians of Central America with narrow ranges have declined, leading to increased IUCN Red List status (e.g. *Atelopus* spp.), and possibly even extinction (e.g. *Incilius periglenes*). Widespread species exposed to the same threats may decline locally, but not enough throughout their range to increase their extinction risk. Furthermore, species with restricted ranges are often specialists, which has been associated with declines in several taxa (Clavel et al., 2011) including frogs (Cooper et al., 2008). Narrow tolerance to environmental conditions makes species highly susceptible to climatic change or fluctuations (Murray and Hose, 2005).

Large body size has been found to correlate with population declines in mammals (Tomiya, 2013), birds (Owens and Bennett, 2000) and amphibians (Lips et al., 2003). Lips et al. (2003) suggested that body size might regulate population density. For example, large-bodied frogs would be at a disadvantage because, all else being equal, they would have a lower density than small frogs and, since population density may influence population survival, larger frogs might be less resilient to habitat alteration. Considering the interaction with clutch size, species with larger body sizes but average-size clutches may not reach a density that ensures survival if habitat disturbances occur.

Family was identified as the main predictor of decreasing population trends. Lotic breeding habits and association with forest or rupestrian habitats were also important predictors of population decline. The 5 families with increased probability of population decline are associated with forest habitats and/or have lotic breeding habits. While these associations have already been explained in relation to vulnerability, the fact that taxonomy played the most important part in this model may be masking a bias of the scientific community towards forest-associated amphibians, since this proxy was derived from quantitative data more widely available from forest species. González-Suárez et al. (2012) identified biases in the spatial distribution of data availability, especially in the diverse tropics, where disparity in data availability was greater among species. The authors found published studies focused on a small group of species, often those easily sampled or more attractive. Multivariate analyses that consider several traits associated with vulnerability to extinction are

likely limited to a skewed subset of species that may not be representative of the whole ensemble. Although this does not imply that all comparative analyses are mistaken or erroneous, it must be used to motivate more unbiased data gathering.

Intrinsic traits were strong predictors of extinction risk, while variables describing direct human impacts apparently had no effect on extinction risk. One plausible explanation for this finding is that populations of threatened species may have already been extirpated from the most disturbed habitats before assessments occurred (Cardillo et al., 2005; Tingley et al., 2013). Another possibility is that detrimental effects of anthropogenic activities have broad, across-species consequences, being detrimental to all species. In this case, variables describing human impacts are not identified as mediators of extinction risk because they affect a wide range of species.

The Red List is often used as the main tool for setting priorities for conservation measures. Although the system is valuable and reliable, it has its limitations, and may under- or over-estimate extinction risk for certain taxa (IUCN, 2001), rendering the category of threat insufficient to determine conservation priorities. Other aspects, such as biological characteristics of the subject, should be considered during this process (IUCN, 2001). There is a need for integrative, predictive and spatially-explicit frameworks capable of accurately identifying species at higher risk, evaluating the consequences of disturbances for biodiversity and guiding conservation actions, especially in biodiverse, highly disturbed and scarcely studied regions.

Our study suggests that the extinction risk of amphibians worldwide may be severely underestimated, especially in scarcely studied and highly anthropogenic biomes. We found that a large proportion of species predicted as sensitive and/or decreasing is currently listed as LC or DD by the Red List. This corroborates previous studies regarding other taxa; smaller, unpopular and inconspicuous species may be severely unacknowledged by the world's leading extinction risk classification system, despite their often pivotal importance for ecosystem functioning. Bland et al. (2014) found that 64% of the world's mammals categorized as DD were actually predicted as threatened and Butchart and Bird (2010) and Morais et al. (2013) underscored the urgency to consider DD species as priorities for studies. In fact, DD amphibians are likely to be more threatened with extinction than their fully assessed

counterparts (Howard and Bickford, 2014). Given their importance for ecosystem functioning and the intrinsic difficulties in studying amphibians, predictive integrative trait-based analyses may give us insight into impending declines and prioritize regions for scientific projects or conservation actions.

About 70% of the species analyzed are major conservation gaps, while only 29 species are sufficiently protected. The center of the Cerrado is the biome's main hotspot for high extinction-risk anurans, which may be partially explained by the high concentration of narrow endemics in mountainous regions, such as Serra do Cipó (e.g., *Bokermannohyla saxicola* and *Hypsiboas cipoensis*), Serra do Cabral (e.g., *Scinax cabralensis*), Serra da Canastra (e.g., *Bokermannohyla ibitiguara* and *Scinax maracaya*), Chapada dos Veadeiros (e.g., *Hypsiboas ericae* and *Leptodactylus tapiti*), and Chapada dos Guimarães (e.g., *Phyllomedusa centralis*, *Pristimantis crepitans*) (Valdujo et al., 2012). A further explanation may be the historical human occupation of that region, coupled with the inadequacy of the local PA network. We conclude that the extinction risk of the Cerrado anurans appears severely underestimated, and the current PA network is insufficient to protect at least 50% of the minimum area required for ensuring the protection of 141 species. *Bokermannohyla ibitiguara, Bokermannohyla izecksohni, Elachistocleis bumbameuboi, Hypsiboas ericae, Pristimantis crepitans, Proceratophrys moratoi, Phyllomedusa oreades, Rhinella scitula,* and *Scinax cabralensis* have especially high conservation needs, and <10% of their conservation target achieved. These species are concentrated mainly in the southwest and central regions of the biome. Hence, we recommend that these species and regions in particular be prioritized for conservation actions in the Cerrado.

Our results provide novel insights into factors that lead to a high risk of extinction in anurans, highlighting the usefulness of an integrative framework for making predictions regarding the likelihood of future population declines. This study underscores the urgency of taking more specific and integrative approaches, considering species ecology and landscape metrics with powerful quantitative tools to unveil the patterns that lead to extinction, and use those results to guide conservation and management policies. The cost-effective approach we present may be of special value for biodiverse regions, with strong anthropogenic pressure, but weak government support and scarce funding for conservation actions. Brazil is currently

experiencing extremely high economic demands, and after long decades of raising public awareness to the importance of protecting the Amazon rainforest, other biomes have been targeted to fulfill the high social and economic exigencies (Allan, 2003). Non-forest biomes, such as the Cerrado, have been neglected, even though they cover large parts of the country and have biodiversity levels comparable to forests (Overbeck et al., 2015). To avoid losing much of its biodiversity and ecosystem services, conservation and sustainable land use policies in Brazil need to be extended to non-forest biomes, encompassing the creation of new large protected areas, the reinforcement of legal restrictions of land use; extension of subsidy programs and governance commitments to non-forest biomes; and the improvement of ecosystem monitoring, management and sustainable use in non-forest biomes (Overbeck et al., 2015). Indeed, if Brazil manages to extend its conservation successes to non-forest biomes, it not only would contribute significantly to conservation of its biodiversity, but also could take the lead in conservation of non-forest biomes worldwide. Frameworks such as ours may shed light into which areas and species need more protection and what is the minimum protection each species needs to endure. These practical approaches may be vital in prioritizing conservation actions in the most neglected non-forest biomes. However, these efforts should be accompanied by substantial increases in coordinated research on the long-term monitoring of amphibian populations and collection of life history and ecological data to further understand species declines and mitigate current threats.

3.6. Conclusion

The extinction risk of certain taxa and biomes is possibly underestimated worldwide. This may be especially dangerous for highly sensitive taxa from highly diverse but anthropogenic regions. Although the value of the Red List is unquestionable, its generalist character requires the use of other complementary approaches to accurately assess and predict extinction risk, to prioritize conservation actions. The Red List very clearly warns of the system's limitations, stating that it should not be used as the sole instrument for approaching conservation prioritization. Our study shows that adopting an integrative specific approach to evaluate extinction risk, using species traits in association with threat exposure, may be an accurate and cost-effective framework. We do not intend to suggest transformations to the Red

List, but rather motivate the use of holistic, informed and more specific approaches, that capitalize the Red List's value and ensure successful outcomes, especially for biodiversity hotspots. Planning and implementing conservation actions takes large amounts of time, effort and funding. The framework we presented may be particularly valuable to prioritizing conservation actions in biomes with important conservation value, high human pressure and low funding.

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Supplementary material

Table A1. Predictors used to assess anuran extinction risk. For each species trait or extrinsic environmental variable considered. respective attributes. definition and relevance for this study are stated.

Predictor variables		Attribute	Definition	Relevance
Intrinsic biological/ecological traits	**Family**	Aromobatidae	Taxonomic family	Extinction risk is not phylogenetically random. and species traits are the product of shared evolutionary history. Hence. we used the taxonomic category family to assess threats among related species.
		Brachycephalidae		
		Bufonidae		
		Centrolenidae		
		Ceratophryidae		
		Craugastoridae		
		Cycloramphidae		
		Dendrobatidae		
		Hylidae		
		Hylodidae		
		Leptodactylidae		
		Microhylidae		
		Odontophrynidae		
		Pipidae		
		Ranidae		
	Activity	Diurnal	Adults more active during	The period during which a species is

Predictor variables		Attribute	Definition	Relevance
			the day.	more active may determine how intensely the individuals will be affected by anthropic activities. e.g. individuals active during the period of disturbance will be more affected than those sheltered.
		Nocturnal	Adults more active during the night.	
		Diurnal & nocturnal	Adults are active during day and night.	
	Habits	Terrestrial	Adults associated with terrestrial strata	Defines the environmental/vertical stratum with which the species is more strongly associated. The typical location of a species determines if and how intensely it will be affected by anthropic activities.
		Arboreal	Adults often found perched on herbaceous or arboreal vegetation.	
		Aquatic	Adults associated with aquatic environments	
		Semi-aquatic	Adults associated with both terrestrial and aquatic	

Predictor variables		Attribute	Definition	Relevance
			environments	
	Fossorial behaviour	Presence/Absence	Adults remain buried during part of the year. It is not dependent on a species' habit. i.e. there are aquatic and terrestrial species with fossorial behaviors.	The ability that some species have to remain buried during periods of time with unfavorable environmental conditions may protect it from some anthropic activities.
	Snout-vent-length (SVL)	Continuous variable (mm)	Distance measured in millimeters from an individual's snout to its vent. Values used for this study are average values of males and females.	Larger species are commonly associated with high water deficit areas. whereas the smallest are usually found in humid areas. Anuran body size gradients reflect effects of reduced surface to volume ratios in larger species to control both heat and water balance (Olalla-Tárraga et al. 2009). Resistance to

Predictor variables		Attribute	Definition	Relevance
				desiccation also relates to mobility. Larger species forced to migrate across agricultural matrices. from shelter areas to breeding areas. may be more successful than smaller ones.
	Habitat	Open areas	Species typical of areas dominated by herbaceous species. with few sparse trees. e.g. savannas. grasslands.	A species habitat-type will determine if and how intensely a species is affected by anthropic activities. For example. a species may have traits correlated with high vulnerability to habitat alteration but if the habitat is unattractive for anthropic activities. it may remain unaffected.
		Forested areas	Species typical of areas dominated by trees.	
		Rupestrian fields	Species typical of high altitude areas dominated by rocks. herbaceous	

Predictor variables		Attribute	Definition	Relevance
			species and very sparse trees. Typical cerrado physiognomy.	
		Open areas & forested areas	Species commonly found in both forested and open areas.	
	Breeding site	Lentic water bodies	Species that breed in lentic water bodies such as ponds.	Breeding sites determine the degree of dependence on aquatic and terrestrial environments and. consequently. how intensely species are affected by anthropic pressures.
		Lotic water bodies	Species that breed in lotic water bodies such as streams.	
		Lentic & lotic water bodies	Species that breed in lentic and lotic water bodies	
		Land	Species that breed in terrestrial	

Predictor variables		Attribute	Definition	Relevance
			environments. such as the leaf-litter.	
		Land & lotic waterbodies	Species that lay the clutch in terrestrial environments. such as the leaf-litter but transport the larvae to streams.	
	Breeding strategy	Free eggs & larvae	Both clutch and tadpoles are free in aquatic environments	Breeding strategy may be one of the most important traits in determining a species' vulnerability to agricultural activities. It is during the egg and larval stage that amphibians are especially vulnerable to environmental factors such as dehydration. UV light. predation or agrochemicals. Breeding
		Protected eggs	Egg clutch is protected. e.g. in the leaf litter.	
		Foam nests exposed	Egg clutch protected by a foam nest exposed. e.g. on the water surface	

Predictor variables		Attribute	Definition	Relevance
		Foam nests protected	Egg clutch protected by a foam nest that remains unexposed. e.g. in subterranean chambers.	specialization (e.g.. foam nests. arboreal eggs. terrestrial eggs. direct development) is. therefore. very important when assessing a species' vulnerability to disturbances.
		Clutches in vegetation or rocks	Egg clutches placed in leaves or rocks. Upon hatching. tadpoles fall or move to aquatic environments.	
		Direct development	Direct development of tadpoles with emergence of small frogs.	
	Clutch size	Continuous variable	Average number of eggs per clutch	Clutch size determines the probability of no recruitment as a result of anthropic activities. Species with unspecialized breeding modes may be more likely to produce

Predictor variables		Attribute	Definition	Relevance
				offspring because of their large clutches. despite the exposure of eggs and tadpoles to the environment.
	Parental Care	Present	Some form of parental care present. such as egg/tadpole attendance or tadpole transport.	The presence of some form of parental care increases the survival probability of clutches and tadpoles. which may be important in unstable anthropic environments.
		Absent	No form of parental care. Clutches and tadpoles are left unattended	
	Breeding Season	Rainy season	Species that breed during the dry season (May - September).	In the amphibian biphasic life cycle. the egg and larval stages are the most vulnerable to environmental factors. Therefore. a species' breeding time may determine how
		Dry Season	Species that breed during the rainy season	

Predictor variables		Attribute	Definition	Relevance
			(October - April).	intensely it is affected by agricultural activities.
		Dry & rainy season	Species that breed during both dry and rainy seasons.	
	Breeding pattern	Prolonged	Species that breed for at least 3 months.	Breeding periods may determine how sensitive a species is to unstable environments. Species with explosive breeding habits may have a greater probability of successfully reproducing than species that require specific conditions to breed and. despite breeding for longer periods. typically have smaller clutches and take longer to complete development.
		Explosive	Species that breed for less than 3 months.	
		Prolonged & explosive	Species that breed during less than 3 months in some habitats but during more than 3 months in other habitats.	
	Range area	Continuous variables	Total distribution of the species in	The distributional area of a species determines i) to which

Predictor variables		Attribute	Definition	Relevance
			km^2.	activities it is exposed and ii) how activities will impact the populations. i.e. species with small ranges are more likely to suffer declines than more widespread species.
	% Range area in the Cerrado		% of the total range area of the species that is included in the Cerrado.	Because this study considers the anurofauna of the Brazilian Cerrado. we describe the degree of association of each species with the biome. Species with a greater part of their range in the biome will be more impacted by ongoing anthropic activities.
Extrinsic environmental variables	**% Range area with natural vegetation**		% of the Cerrado species range occupied by natural vegetation.	The percentage of the species' area occupied by natural vegetation may describe how exposed a species is to anthropic pressure.

Predictor variables		Attribute	Definition	Relevance
	% Range area occupied by crops		% of the Cerrado species range occupied by crops.	The percentage of the species' area occupied by crops describes how exposed a species is to this anthropic pressure.
	% Range area occupied by pastures		% of the Cerrado species range occupied by pastures.	The percentage of the species' area occupied by pastures describes how exposed a species is to this anthropic pressure.

Table A2. List of the 195 extant species of anurans in the Cerrado with respective compiled and predicted vulnerability (S - sensitive; T- tolerant; U- unknown). population trend (S-stable; D-decreasing and U-unknown) and original IUCN Red List status (LC- Lest Concern; DD - Data Deficient; CR - Critically Endangered; NT - Near threatened).

Species	Vulnerability	Predicted Vulnerability (RF)	Population trend	Predicted Population Trend (RF)	IUCN
Adelphobates galactonotus	U	S	S	S	LC
Adenomera bokerman ni	T	T	S	S	LC
Adenomera hylaedactyla	T	T	S	S	LC
Adenomera marmorata	T	T	S	S	LC
Adenomera martinezi	T	T	S	S	LC
Adenomera picta	U	S	S	S	LC
Allobates brunneus	S	S	U	S	LC
Allobates femoralis	T	T	S	S	LC
Allobates goianus	U	S	U	S	DD
Ameerega braccata	S	S	U	S	LC
Ameerega flavopicta	S	S	S	S	LC
Aplastodicus perviridis	T	T	S	S	LC
Aplastodiscus ibirapitanga	T	T	U	S	LC
Aplastodiscus leucopygius	T	T	S	S	LC
Barycholos ternetzi	S	S	D	S	LC
Bokermannohyla alvarengai	U	S	S	S	LC
Bokermannohyla ibitiguara	S	S	U	S	DD
Bokermannohyla izecksohni	S	S	D	S	CR
Bokermannohyla martinsi	S	S	S	S	LC
Bokermannohyla nanuzae	S	S	S	S	LC
Bokermannohyla pseudopseudis	S	S	D	S	LC
Bokermannohyla sagarana	U	S	S	S	NT
Bokermannohyla saxicola	S	S	D	D	LC
Bokermannohyla sazimai	S	S	U	D	DD
Ceratophrys aurita	U	T	D	D	LC
Ceratophrys cornuta	U	T	S	S	LC

Ceratophrys cranwell	T	T	D	S	LC
Ceratophrys mehelyi	U	T	U	S	DD
Chiasmocleis albopunctata	T	T	S	S	LC
Corythomantis greeningi	U	T	S	S	LC
Crossodactylus bokermanni	S	S	D	D	DD
Dendropsophus anataliasiasi	T	T	S	S	LC
Dendropsophus araguaya	U	S	U	S	DD
Dendropsophus branneri	T	T	S	S	LC
Dendropsophus cerradensis	U	T	U	S	DD
Dendropsophus cruzi	T	T	S	S	LC
Dendropsophus elegans	T	T	S	S	LC
Dendropsophus elianeae	U	T	U	S	LC
Dendropsophus leucophyllatus	U	T	S	S	LC
Dendropsophus microcephalus	T	T	I	S	LC
Dendropsophus microps	U	T	S	S	LC
Dendropsophus minutus	T	T	S	S	LC
Dendropsophus nanus	T	T	S	S	LC
Dendropsophus rubicundulus	S	S	D	S	LC
Dendropsophus sanborni	T	T	S	S	LC
Dendropsophus soaresi	U	T	S	S	LC
Dendropsophus tritaeniatus	S	S	S	S	LC
Dermatonotus muelleri	S	S	S	S	LC
Elachistocleis bicolor	T	T	S	S	LC
Elachistocleis bumbameuboi	U	S	U	S	DD
Elachistocleis matogrosso	U	S	U	S	LC
Elachistocleis piauiensis	T	T	S	S	LC
Eupemphix nattereri	S	T	D	S	LC
Haddadus binotatus	U	T	S	S	LC
Hydrolaetare schmidti	U	T	S	S	LC
Hylodes otavioi	U	S	U	D	DD
Hypsiboas albomarginatus	T	T	S	S	LC
Hypsiboas albopunctatus	T	T	S	S	LC

Hypsiboas boans	U	T	S	S	LC
Hypsiboas buriti	S	S	U	S	DD
Hypsiboas caingua	T	T	S	S	LC
Hypsiboas cipoensis	U	T	D	S	NT
Hypsiboas crepitans	T	T	S	S	LC
Hypsiboas ericae	U	S	U	D	DD
Hypsiboas faber	T	T	S	S	LC
Hypsiboas fasciatus	U	T	S	S	LC
Hypsiboas geographicus	U	T	S	S	LC
Hypsiboas goianus	T	T	D	S	LC
Hypsiboas lanciformis	S	S	D	D	LC
Hypsiboas multifasciatus	U	T	S	S	LC
Hypsiboas phaeopleura	S	S	U	D	DD
Hypsiboas polytaenius	T	T	S	S	LC
Hypsiboas prasinus	U	T	S	S	LC
Hypsiboas punctatus	T	T	S	S	LC
Hypsiboas raniceps	T	T	S	S	LC
Ischnocnema juipoca	T	T	S	S	LC
Ischnocnema nasuta	U	T	D	S	LC
Ischnocnema penaxavantinho	T	T	U	S	DD
Itapohyla langsdorffii	S	S	D	D	LC
Leptodactylus bolivianus	T	T	S	S	LC
Leptodactylus bufonius	T	T	S	S	LC
Leptodactylus camaquara	U	T	U	S	DD
Leptodactylus chaquensis	T	T	U	S	LC
Leptodactylus cunicularius	U	T	S	S	LC
Leptodactylus elenae	T	T	U	S	LC
Leptodactylus furnarius	T	T	S	S	LC
Leptodactylus fuscus	T	T	S	S	LC
Leptodactylus gracilis	T	T	S	S	LC
Leptodactylus knudseni	T	T	S	S	LC
Leptodactylus labyrinthicus	T	T	S	S	LC

Leptodactylus latrans	T	T	S	S	LC
Leptodactylus lineatus	T	T	S	S	LC
Leptodactylus mystaceus	T	T	S	S	LC
Leptodactylus mystacinus	T	T	S	S	LC
Leptodactylus notoaktites	T	T	S	S	LC
Leptodactylus pentadactylus	U	T	S	S	LC
Leptodactylus petersii	T	T	S	S	LC
Leptodactylus podicipinus	T	T	S	S	LC
Leptodactylus pustulatus	T	T	S	S	LC
Leptodactylus sertanejo	T	T	U	S	LC
Leptodactylus syphax	S	T	S	S	LC
Leptodactylus tapiti	U	S	U	S	DD
Leptodactylus vastus	T	T	U	S	LC
Lithobates palmipes	U	T	S	S	LC
Odontophrynus americanus	T	T	S	S	LC
Odontophrynus cultripes	T	T	S	S	LC
Odontophrynus salvatori	S	S	D	S	DD
Osteocephalus taurinus	S	S	S	S	LC
Phasmahyla jandaia	S	S	S	S	LC
Phyllomedusa araguari	T	T	U	S	DD
Phyllomedusa ayeaye	U	T	U	S	CR
Phyllomedusa azurea	T	T	U	S	DD
Phyllomedusa burmeisteri	T	T	S	S	LC
Phyllomedusa centralis	S	S	U	S	DD
Phyllomedusa hypochondrialis	T	T	S	S	LC
Phyllomedusa nordestina	U	T	U	S	DD
Phyllomedusa oreades	U	S	U	D	DD
Phyllomedusa sauvagii	S	S	S	S	LC
Phyllomedusa tomopterna	S	S	S	S	LC
Phyllomedusa vaillantii	U	S	S	D	LC
Physalaemus albifrons	U	T	S	S	LC
Physalaemus albonotatus	T	T	S	S	LC

Physalaemus biligonigerus	T	T	S	S	LC
Physalaemus cicada	U	T	S	S	LC
Physalaemus cuvieri	T	T	S	S	LC
Physalaemus deimaticus	S	S	U	S	DD
Physalaemus ephippifer	T	T	I	S	LC
Physalaemus evangelistai	S	S	U	S	DD
Physalaemus gracilis	T	T	S	S	LC
Physalaemus marmoratus	S	S	U	S	LC
Physalaemus olfersii	U	T	S	S	LC
Physaleamus centralis	S	S	U	S	LC
Pipa pipa	U	T	S	S	LC
Pleurodema diplolister	T	T	S	S	LC
Pristimantis crepitans	U	S	U	S	DD
Pristimantis dundeei	S	S	U	S	DD
Pristimantis fenestratus	U	T	S	D	LC
Proceratophrys boiei	T	T	S	S	LC
Proceratophrys cururu	U	T	U	S	DD
Proceratophrys moratoi	S	S	D	D	CR
Pseudis bolbodactyla	U	T	U	S	LC
Pseudis caraya	U	T	S	S	LC
Pseudis distincta	U	T	D	D	LC
Pseudis fusca	T	T	U	S	LC
Pseudis limellum	S	S	S	S	LC
Pseudis paradoxa	U	T	S	S	LC
Pseudis platensis	U	T	U	S	DD
Pseudis tocantins	U	T	U	S	LC
Pseudopaludicola boliviana	U	T	S	S	LC
Pseudopaludicola falcipes	T	T	S	S	LC
Pseudopaludicola mineira	T	T	U	S	DD
Pseudopaludicola mystacalis	T	T	S	S	LC
Pseudopaludicola saltica	T	T	S	S	LC
Pseudopaludicola ternetzi	T	T	S	S	LC

Rhinella cerradensis	S	S	U	S	DD
Rhinella granulosa	U	T	S	S	LC
Rhinella guttatus	S	S	S	S	LC
Rhinella icterica	T	T	S	S	LC
Rhinella margaritifera	T	T	S	S	LC
Rhinella marina	T	T	I	S	LC
Rhinella ocellata	S	S	D	S	LC
Rhinella ornata	T	T	U	S	LC
Rhinella pombali	T	T	U	S	LC
Rhinella rubescens	T	T	S	S	LC
Rhinella schneideri	T	T	I	S	LC
Rhinella scitula	T	T	U	S	DD
Rhinella veredas	T	T	U	S	LC
Scinax acuminatus	T	T	S	S	LC
Scinax cabralensis	U	S	U	S	DD
Scinax canastrensis	T	T	U	D	DD
Scinax centralis	S	S	D	S	LC
Scinax constrictus	U	T	U	S	LC
Scinax curicica	U	S	U	S	DD
Scinax eurydice	T	T	S	S	LC
Scinax fuscomarginatus	T	T	S	S	LC
Scinax fuscovarius	T	T	S	S	LC
Scinax hiemalis	S	S	D	S	LC
Scinax longilineus	U	S	D	S	LC
Scinax luizotavioi	T	T	S	S	LC
Scinax machadoi	S	S	S	S	LC
Scinax maracaya	U	S	U	S	DD
Scinax nasicus	T	T	S	S	LC
Scinax pinima	S	S	D	S	DD
Scinax rizibilis	S	S	D	S	LC
Scinax ruber	T	T	S	S	LC
Scinax squalirostris	T	T	S	S	LC

Scinax tigrinus	T	T	S	S	LC
Scinax x-signatus	T	T	S	S	LC
Sphaenorhynchus caramaschii	U	T	S	S	LC
Thoropa miliaris	U	T	S	S	LC
Trachycephalus imitatrix	S	S	D	S	LC
Trachycephalus nigromaculatus	T	T	S	S	LC
Trachycephalus venulosus	T	T	S	S	LC
Vitreorana eurygnatha	S	S	D	D	LC
Vitreorana uranoscopa	S	S	D	D	LC

“There is something fundamentally wrong
in treating the Earth as if it were
a business in liquidation.”
Herman E. Daly

Chapter 4

Evidence of anuran community disruption on rice crops: a multidimensional evaluation

4. EVIDENCE OF ANURAN COMMUNITY DISRUPTION ON RICE CROPS: A MULTIDIMENSIONAL EVALUATION.

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4.1. Abstract

Agricultural expansion is a major driver of biodiversity loss, especially in the megadiverse tropics. Rice is the world's most important food crop, but the effects of habitat conversion to rice crops on biodiversity have not been consensual. Nonetheless, given its nature, location and extension worldwide, irrigated rice fields are invariably used by the native fauna. Here we conduct an integrative evaluation of the effects habitat conversion to irrigated rice crops has on anuran communities in a Cerrado-Amazon ecotone. We found that habitat conversion and agricultural management caused profound alterations to the anuran community, namely dramatic loss of species diversity and functional richness with increased functional divergence. Community composition was altered, with dominance by generalist and low representation of specialist. Anuran communities in rice fields exhibited decreased phylogenetic diversity and mean phylogenetic distance, with increased mean nearest phylogenetic distance. Agricultural communities are composed of phylogenetically related species. Nonetheless, taxonomic diversity did not vary significantly, suggesting that it should not be used without complementary metrics. We found small geographic ranges, habitat specialization, small

clutches and large body size to be associated with low species abundances in rice fields. Frogs from crops exhibited lower body condition across guilds, indicating reduced fitness and suggesting that reproductive output and survival may be impaired in these communities. Understanding how communities are altered by human activities will allow better predictions of the functional effects of anthropogenic land-use. Maintaining high levels of diversity in anthropogenic environments is important for ecosystem resilience because diverse communities are more likely to hold multiple species capable of contributing to a single ecological function. Conversion of Neotropical natural vegetation to vast irrigated rice crops results in the extinction of large subsets of species irrespective of their specialization, with even the more resilient generalists exhibiting lower body condition. Neotropical rice crops appear unable to support functionally and phylogenetically diverse, healthy communities, contributing to lower ecosystem resilience and dramatic implications for global ecology, economy and public health.

Keywords: Neotropics, Amphibians, Agriculture, Functional diversity, Phylogenetic diversity.

4.2. Introduction

Deforestation is a major driver of biodiversity loss, especially in the megadiverse Neotropics, where it is mainly caused by agricultural expansion (García-Barrios et al., 2009). Agriculture and cattle farming are known to cause extensive and complex alterations to communities and ecosystems (Frishkoff et al., 2014; Williams-Guillén and Perfecto, 2010). For example, several studies have reported negative effects of habitat conversion to irrigated rice crops on biodiversity (e.g. Attademo et al. 2011; Hyne et al. 2009; Maximiliano Attademo et al. 2015). However, these agricultural wetlands have also been considered valuable for birds and amphibians (Bambaradeniya and Amarasinghe, 2004; Czech and Parsons, 2002; Elphick and Oring, 2003; Lepš et al., 2006) and even functional equivalents to natural wetlands.

Wetlands are important breeding habitats for many amphibian species and irrigated rice fields are invariably used by local amphibians to forage and reproduce. Due to their biphasic life cycle, highly permeable skin and ectothermic physiology, amphibians are very dependent on environmental quality and vulnerable to its change (Niemi and McDonald, 2004). They play keystone roles in ecosystem functioning, acting as both predators and prey, enable nutrient transport between aquatic and terrestrial systems and are among the most diverse and abundant vertebrates, especially in the Neotropics. Amphibians can hence be used as reliable surrogates to evaluate the effects of human disturbances on whole communities and ecosystems (Davic and Welsh, 2004).

Rice is the world's most important food crop, occupying 11% of the world's total arable land (Guimarães, 2009). Asian countries are responsible for 90% of the world's rice production, while Latin America and the Caribbean produce 4.1%, half of which comes solely from Brazil (FAO, 2011). Given the extension and location of rice fields worldwide, determining if these agricultural wetlands can function adequately to maintain biodiverse and healthy communities is of the utmost concern. This takes special significance in the Neotropics, where rice production meets important social and economic demands and biodiversity is especially high and unique.

The effects of anthropogenic landscape modification are complex, often involving the rise of new environmental, compositional and configurational conditions that affect biodiversity. This concept, defined as environmental filtering, suggests that the environment acts as a filter, favoring certain species with particular traits over others

(Keddy 1992; Weiher & Keddy 1995; Mayfield et al. 2005; Lebrija-Trejos et al. 2010). The environmental filters arisen as a consequence of disturbances often favor generalist species while creating communities with species richness similar and even higher to that of pristine environments. General patterns of environmental filtering have been identified for birds, plants, and freshwater organisms. Traits such as body size, leaf area and geographic range have been identified as determinant for species resiliency to disturbances (Lindenmayer & Montague-Drake 2008, McIntyre 2008, Poff 1997). Environmental filtering may hold great promise as a predictive framework to assist conservation planning and management of anthropogenic environments directed at favoring species with particular traits associated with decreased resilience (Hanspach, 2012).

Species richness metrics rely on the erroneous assumption that all species are equal, i.e., only relative abundances establish the relative importance of species in communities and ecosystems (Magurran, 2004). In fact, some species carry more evolutionary history or functional traits essential to ecosystem processes than others (Cadotte et al., 2010; Mouillot et al., 2013a). Nonetheless, most studies addressing community assembly in human-modified landscapes rely on simplistic taxonomic metrics (Sodhi and Ehrlich, 2010) and leave important ecosystem-level consequences unaddressed. Because the complex effects of environmental variation induced by human activities on species is ultimately mediated by specific characteristics (e.g. physiological constraints, habitat requirements, dispersal abilities), considering only taxonomic metrics may fail to provide accurate conclusions on the real consequences of anthropization on biodiversity. To attain more representative conclusions on the effects human activities have on communities, we must go beyond species number and account for different components of biodiversity.

Functional (FD) and phylogenetic diversity (PD) are estimates of biodiversity based on ecological functions and evolutionary histories of species, respectively. FD describes the variability in ecological attributes among species and expresses ecosystem resistance, resilience and functioning (Petchey and Gaston, 2006). FD can be divided into three primary components – functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve). FRic represents the amount of functional space occupied by a species assemblage. FEve corresponds to how regularly species abundances are distributed in the functional space. Finally, FDiv defines how far high species abundances are from the center of the functional space. These facets are complementary and jointly describe the

distribution of species and their abundances within the functional space. PD measures the evolutionary differences among species based on times since divergence from a common ancestor (Faith, 1992), representing an estimate of phylogenetically conserved ecological and phenotypic differences among species (Cavender-Bares et al. 2009). This dimension may characterize the long-term evolutionary potential of specific clades to respond or adapt to current and future environments. Few studies have explored the influences of anthropogenic landscapes on FD or PD (Tscharntke et al., 2012), and most of which have focused on plant and invertebrate assemblages (e.g., Arroyo-Rodríguez et al. 2012; Aviron et al. 2005; Laliberte et al. 2010).

Other metrics have been proposed to assess the effects of anthropogenic disturbance on communities. Body condition is considered an indicator of environmental stress, prey availability and/or habitat quality (Sztatecsny and Schabetsberger, 2005), reproductive investment (Castellano et al., 2004), parasite load, investment in secondary sexual characters (Green, 2001), mate choice (Uetz et al., 2002), survival (Hoey and McCormick, 2004), vulnerability to predation (Murray, 2002), and/or fighting ability (Bee et al., 2000). Body condition is thus a proxy of energy reserves (Schulte-Hostedde et al., 2005) and may be used to assess the effects of environmental disturbances on the individual fitness level.

Here we conduct an integrative evaluation of the effects that habitat conversion to rice fields has on anuran communities in a Cerrado-Amazon ecotone. This region has three large rivers, Araguaia, Formoso and Javaés, hosting the world's largest continuous area of irrigated rice, with over 500.000 ha. As an ecotone, it has unique biodiversity, resulting from constant and historical direct contact between species typical of the Cerrado and the Amazon biomes. We adopted a multidimensional approach to assess i) how taxonomic diversity, species richness and evenness are modified; ii) how functional and phylogenetic diversity are affected; iii) which anuran traits are selected and excluded in Neotropical agricultural landscapes; and iv) use body condition indices to assess if population fitness is unaltered by agricultural activities. We expect that indices considering functional and phylogenetic diversity will provide better evaluations of habitat degradation than indices based on species taxonomic identity and abundances, since species–environment relationships are assumed to be mediated via functional traits (e.g., Suding et al. 2008). Furthermore, we expect rice fields to pose different environmental filters on anuran

communities, resulting in more homogeneous communities, with marked selection for certain traits that ensure persistence on these altered landscapes. Finally, we hypothesize that, although generalist species are apparently successful in these environments, body condition indices will be lower than in pristine areas, which may indicate that agricultural environments are unable to host healthy generalist anuran communities. This is the first study to simultaneously assess taxonomic, functional and phylogenetic dimensions of anuran communities, along with body condition, within a human-modified landscape in the Neotropics.

4.3. Methods

4.3.1. Study area

This study took place in the states of Goiás and Tocantins, Brazil. Both pristine and agricultural study areas are inserted in an ecotone region between the Amazon rainforest and the Brazilian savanna, the Cerrado.

Depending on topography, soil type and condition, temperature, pluviometry and available technology, there are five types of rice fields in Brazil. Irrigated and upland rice fields are the most expressive regarding crop area and yield, accounting for 67% and 37% of the annual production, respectively (IBGE, 2005). While upland rice fields are distributed along the biome, on montane areas, irrigated rice is grown in periodically flooded regions, usually close to large rivers. Considered Brazil's "water tank", with its extensive periodically flooded areas, high water availability and suitable climatic and territorial extension, the Cerrado has great agricultural potential for irrigated rice production (Santos and Rabelo, 2004).

Sampled rice fields are located in the municipal district of Lagoa da Confusão (Tocantins). Pristine areas are located in Pium, Ilha do Bananal (Tocantins) and Monte Alto (Goiás). The region is a seasonally flooded area, with two large rivers, Formoso and Javaés, and a very pronounced rainy season from October to April. This highly unique ecotone is often characterized by the presence of *ipucas*, "islands" of closed native vegetation that remain flooded longer than the surrounding areas. Recently, an endemic rodent (*Rhipidomys ipukensis*) was found within these structures (Rocha et al., 2011). When an *ipuca* is destroyed to make place for crops, low crop yields often result because when the native vegetation is removed, the *ipuca* area remains flooded for longer, thus becoming useless for agriculture. The *ipucas* exist only in the state of Tocantins, making the agricultural landscapes of this state quite peculiar, with vast crop areas speckled by many "islands" of native vegetation of variable dimensions.

Irrigated rice fields in the Cerrado-Amazon ecotone present a dynamic hydrologic regime, with variation between aquatic and terrestrial phases. When rice is being produced, from December to April, rice fields have surface water until harvest, before which crops are

completely drained (Santos and Rabelo, 2004). After rice harvesting, fields may remain without crops, or other crops, such as soybeans or watermelons, may be grown, depending on the landowner's will. Besides rice fields, the region's landscape is also occupied by pasture areas, where cattle, emus or water buffalos roam.

Sampled pristine areas are characterized by natural vegetation typical of Cerrado-Amazon ecotone, with no significant anthropogenic activities.

4.3.2. Sampling design

To ensure we represented most of the environmental variability of this agricultural landscape, we chose a total of 10 rice fields along the Rio Formoso irrigation project (Fig. 4.1). Chosen rice fields varied in size, *ipuca* abundance and dimensions and waterbody abundance and size. We selected 4 to 5 lentic waterbodies for anuran sampling in each rice field, totaling 35 waterbodies sampled in rice fields. All waterbodies were located inside the agricultural matrix or less than 50 m from rice fields. Waterbodies for the pristine and agricultural area were chosen based on type, size and hydroperiod. We chose small (25 m^2) to large (1200 m^2) temporary lentic waterbodies. All sampled waterbodies were at least 450 m apart (Fig. 4.1).

4.3.3. Anuran surveys

Agricultural and pristine area surveys were conducted during two rainy seasons, from February 2013 to April 2014. Anuran sampling was performed using nocturnal visual encounter surveys along a 10 m wide margin of each waterbody, for approximately 30 min. Every individual seen perched on the vegetation, on the ground, under the leaf litter, logs or stones was caught, identified, measured, weighed, photographed and then released near the site of origin.

4.3.4. *Trait Data*

We compiled life history and ecological traits for every anuran species encountered in the agricultural and pristine study areas. For each species we compiled information on 12 traits: activity, habits, habitat, fossorial behavior, adult snout-vent length (SVL), breeding site, breeding strategy, clutch size, parental care, breeding season, breeding pattern and geographic range size. Traits were chosen based on perceived importance for determining species resilience to agricultural activities (Table A1) and on data availability. Trait data were

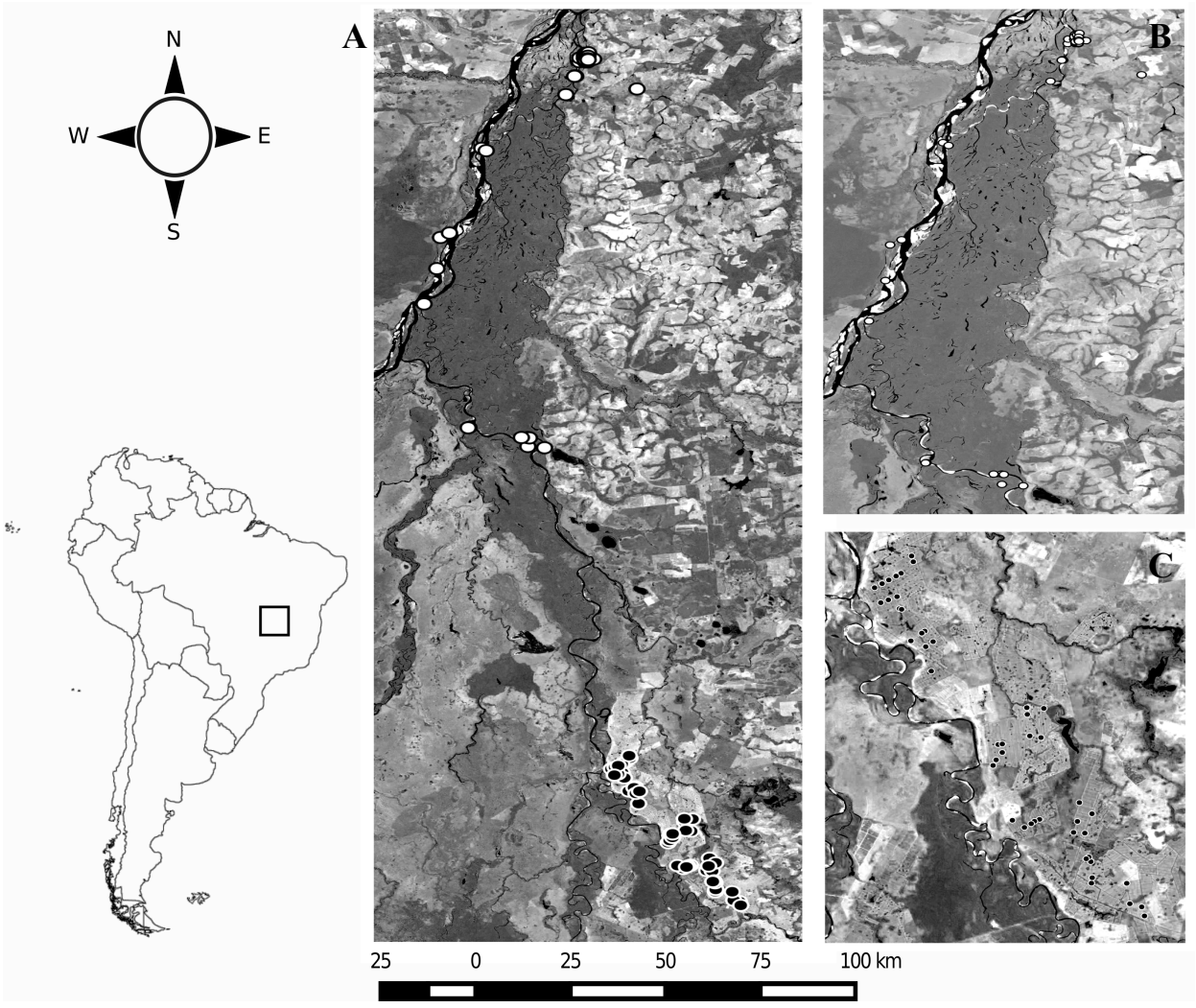

Figure 4.1. Study area (A). Lighter areas represent agricultural lands while darker areas represent native vegetation. White dots represent pristine sampling sites (detailed in B), dark dots represent agricultural sampling sites (detailed in C).

compiled from the literature, the AmphibiaWeb and IUCN online databases. If published data were unavailable, we relied on expert opinion or inferred trait information based on closely related species.

4.4. Data analysis

4.4.1. Sampling efficiency and species richness

To assess the effectiveness of our sampling effort, we fitted species accumulation curves for the agricultural and pristine areas. We calculated observed species richness, estimated species richness (Chao1 estimator), species diversity (Shannon–Weaver's H) and species evenness (Pielou's J) for the agricultural and pristine areas, for every site sampled in both areas, using the Vegan package (Oksanen et al., 2010) in program R version 3.1.2 (Team, 2013).

4.4.2. Taxonomic Diversity

We calculated taxonomic diversity (D) and taxonomic distinctness (D*) (Clarke and Warwick 2001) based on information derived from a hierarchical taxonomic tree. We used taxonomic classification of all species sampled in both agricultural and pristine areas. Taxonomic indices were calculated using package vegan (Oksanen et al., 2010) on program R version 3.1.2 (Team, 2013).

4.4.3. Functional diversity

Mason et al. (2005) divided functional diversity into three independent components: the amount of trait space filled by the community (FRic), the divergence of abundance distribution in the occupied trait space (FDiv) and the evenness of distribution of abundance in trait space (FEve). We quantified functional richness (FRic) according to Villéger, Mason, and Mouillot (2008), which corresponds to the volume inside the hull that contains all trait combinations represented in the community. FRic is only influenced by the identity of species and more particularly by the most extreme species (in terms of functional traits), which delimitate the convex hull. We quantified functional evenness and functional divergence with FEve and

FDiv, proposed by Villéger et.al. (2008). FEve includes both the regularity of species distribution and the regularity of their abundances along the "skeleton" of the functional volume occupied. It decreases when functional distances among species are less even or when abundances are less evenly distributed among species, i.e. when the main abundances belong to functionally close species. FDiv, the third facet of functional diversity, describes whether higher abundances are close to the volume borders. It approaches zero when highly abundant species are very close to the center of gravity of the volume occupied and approaches unity when highly abundant species are very distant from the center of gravity. FDis is the mean distance in multidimensional trait space of individual species to the centroid of all species being unaffected by species richness by construction (Laliberté et al., 2010). We also computed functional group richness (FGR), which returns the number of functional groups per community, as well as the abundance of each group in each community.

All of the abovementioned components of functional diversity were computed for both areas, based on trait values and relative abundances of species. To assess differences among indices from agricultural and pristine areas, we used *t*-tests or Wilcoxon–Mann–Whitney tests for non-parametric data. All FD indices were calculated using packages FD (Laliberté et al., 2015), Ape (Paradis et al., 2004) and Picante (Kembel et al., 2010) in R version 3.1.2 (Team, 2013).

4.4.4. Null model validation

Most changes in FD components cannot be interpreted directly, since communities differ in species richness. Thus, we must assess not if observed diversity indices are significantly different between the agricultural and pristine areas, but if diversity indices are significantly different between agricultural and pristine areas after randomizing the samples between the areas. We tested the null hypothesis of no change in pristine and agricultural communities, designing an appropriate randomization procedure to test community changes in diversity indices (Swenson, 2014). Our null models were independent swap models, which randomize community data, while maintaining species occurrence frequency and sampling species richness for each community. The randomization process was carried out 999 times for each index and area and the P-value associated with the null hypothesis (no community effect)

rejection was estimated (Manly, 2007). We tested whether the actual FD for each community was significantly higher or lower than the null FD distribution, at $\alpha = 0.05$. This approach allowed us to determine if changes in FD simply reflected species richness, or if species composition and trait diversity varied in important ways between agricultural and pristine areas. In addition, a standardized effect size (SES) was calculated for each index and each area to measure the statistical amount of deviation of the observed index of community structure from the distribution of simulated indices (Gotelli and McCabe, 2002). Null models and respective significance metrics were generated on program R version 3.1.2.

4.4.5. Phylogenetic Diversity

We used the phylogenetic tree built by Isaac et al. (2012) from the amphibian 'tree of life' described by Faivovich et al. (2006), with 5713 amphibian species and respective branch lengths. We pruned this supertree to build a smaller phylogenetic tree with every species sampled in the pristine and agricultural areas. All operations related to pruning the original Isaac et al. (2012) supertree were performed on R v. 3.1.2 using package Ape (Paradis et al., 2004). We quantified the phylogenetic diversity (PD) with three different measures: Faith's index of PD (PDf, Faith 1992), mean phylogenetic distance (MPD) and mean nearest phylogenetic taxon distance (MNTD) (Webb et al., 2002). Faith's index of phylogenetic diversity is defined as the minimum total length of the phylogenetic branches connecting the species together on the phylogenetic tree. The abundance-weighted measures MPD and MNTD are respectively the average distance between two random individuals in a sample and the average distance to the closest heterospecific individual for all individuals in the sample (Webb et al., 2008). The branch lengths on the phylogram were used as distance measures. MPD is a measure of the tree-wide phylogenetic relatedness of the community, while MNTD focuses more on the relationships between the tips of the phylogenetic tree (Kraft et al., 2007). Measures of PD were calculated in R version 3.1.2 with the Picante package (Kembel et al., 2010).

4.4.6. Anuran trait association with agricultural landscapes

To identify which traits persisted or were lost with land use, we used machine learning techniques to build classification and regression trees (CART). Although these tools have been previously used in ecology and recommended for conservation practice and wildlife management (Oliver et al., 2012), their application is still limited (Olden et al., 2008). Decision and regression trees are designed to identify nonlinear, context-dependent relationships between multiple correlated predictor variables (Olden et al., 2008). They do not assume a specific distribution of predictor variables or data independence, avoiding potential concerns about pseudoreplication and alleviating the need for explicit phylogenetic control (Bielby et al., 2009). Predictor variables may appear repeatedly in the model as necessary, a fundamental difference from the single-predictor variables of linear models. Finally, these analyses produce graphical outputs that quantify and summarize the interactions in a visual, easily interpretable format.

Because traditional tree models can be unstable, we used random forest, which combines the predictions of many independent decision-tree models to produce robust results regarding variable importance (Breiman, 2001). However, because random forest models do not produce a visual representation of variable importance, we also fitted traditional classification and regression tree models. We used packages randomForest (Liaw and Wiener, 2015) and rpart (Therneau and Atkinson, 1997) of program R v. 3.1.2 to determine the main predictors of anuran presence and species relative abundance in rice fields. Trees are built by repeatedly partitioning the dataset into a nested series of mutually exclusive groups, each group as homogenous as possible regarding the response variable. Homogeneity is measured by the Gini index. Branches or split points in the tree are determined by considering all possible splits of all predictor variables and selecting the split that results in the most homogenous subgroups for the data. The branching process continues until further subdivision no longer reduces the Gini index. Lower branches are afterwards pruned by 10-fold cross-validation to produce an optimal tree, balancing complexity (i.e., number of nodes) with prediction accuracy. The smallest tree with an error rate within 1 standard error of the minimum-error tree is taken as the optimal tree.

We quantified overall model accuracy using the percentage of species correctly classified (PCC), specificity (percentage of species not present correctly classified), and sensitivity (percentage of species present correctly classified). We assessed the accuracy of the relative abundance model using cross-validation from package rpart in program R.

4.4.7. Body condition index

The original method of estimating body condition involved the quantification of fat deposits and was fatal for the studied individuals (Blackwell, 2002). A non-destructive alternative to the above-mentioned method is the use of body condition indices (BCI) based on allometric relationships between length and weight. We extracted body condition indices from the residuals of the regression of log(body mass) on log(snout–vent length) (Jakob et al., 1996; Peig and Green, 2010). To evaluate how body condition varied between pristine and crop areas and across guilds, we calculated body condition indices for two treefrog genera (*Dendropsophus* and *Hypsiboas*) and for a terrestrial genus (*Leptodactylus*). *Hypsiboas* represents larger treefrogs while *Dendropsophus* represents smaller treefrogs. Samples consisted of 241 individuals of *Dendropsophus*, 161 *Hypsiboas* and 657 *Leptodactylus*. Half of the datasets corresponded to individuals from pristine areas, and the other half to individuals sampled in rice fields.

4.5. Results

4.5.1. Sampling efficiency and species richness

Although sampling was effective in capturing the vast majority of the species present in rice fields, sampling effort on pristine areas could have been increased and more species would have been registered (Table 4.1, Fig.A4.1). Species richness was significantly higher in pristine areas than in rice fields (Table 4.1, Fig.A4.2).

4.5.2. Taxonomic Diversity

Differences between taxonomic metrics in pristine and agricultural areas were not significant (Table 4.1).

Table 4.1. Taxonomic indices, species observed and estimated (Chao 1) for pristine and agricultural areas with respective standard errors.

Metric	Pristine areas	Rice fields	P-value
Species observed	44	14	0.017
Species estimated (Chao)	56 (11.14)	14.23 (0.67)	0.010
Proportion of species observed	0.79	0.98	-
Species diversity (H)	2.27 (0.81)	1.60 (0.17)	0.040
Species evenness (J)	0.82 (0.12)	0.73 (0.05)	0.061
Taxonomic diversity	65.58 (16.90)	59.54 (5.53)	0.331
Taxonomic distinctness	80.60 (7.28)	81.71 (3.30)	0.681

4.5.3. Functional diversity

Functional richness was significantly higher in pristine areas than in rice fields ($W=17$, $p= 0.02$). Functional divergence was significantly lower in pristine areas than in rice fields ($t(12.5) = 2.99$, $p=0.01$). Regarding functional trait clusters, cluster 1 only had 40% of the species present in pristine areas represented in rice fields, cluster 2 had 27%, cluster 3 had 31% and cluster 4 had 25% (Fig. 4.2). Cluster 3 was significantly more abundant in pristine areas than in rice fields ($t(3.2607) = 8.47$, $p=0.01$) (Fig.4.3). The NMDS also revealed differences in community composition, with the agricultural community being composed of a few species, strongly associated to those environments,

while the pristine community was composed of more species (Fig. 4.4).

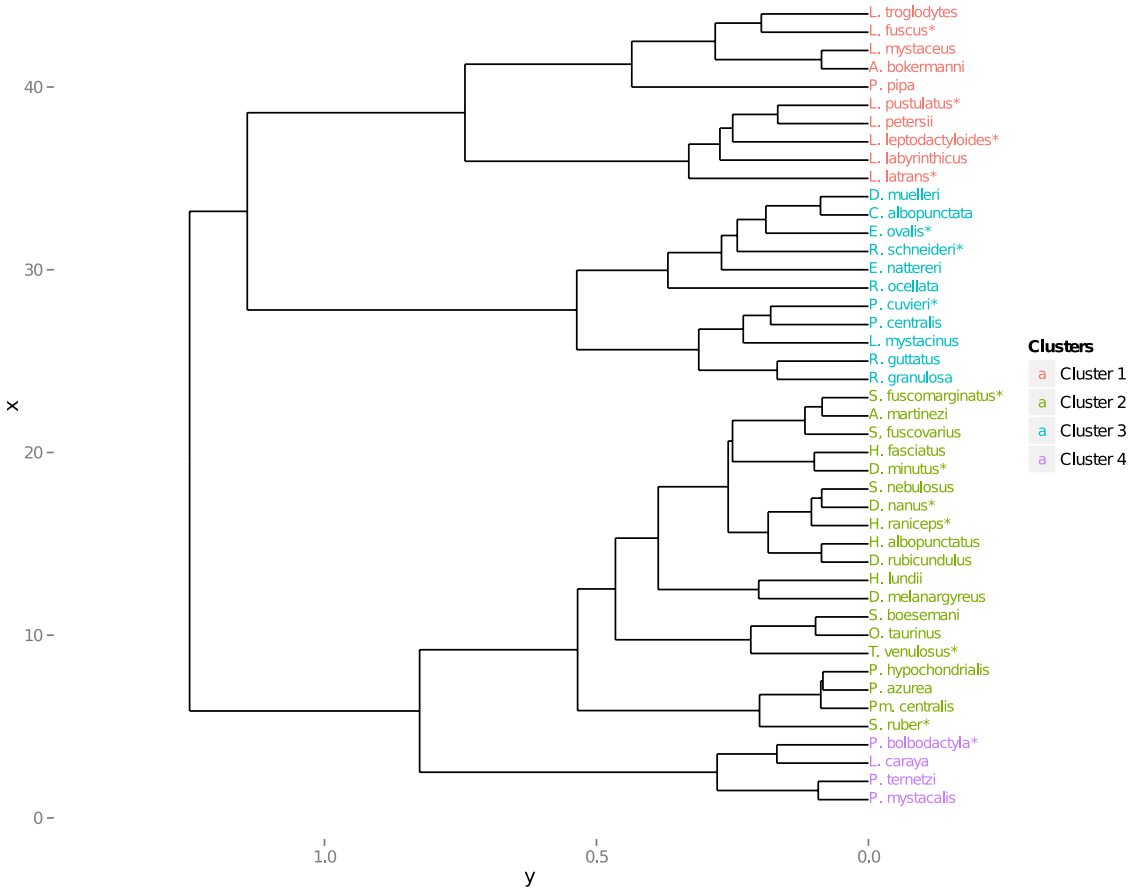

Figure 4.2. Functional trait dendrogram, with every species observed during this study. Species with asterisk are present in agricultural areas.

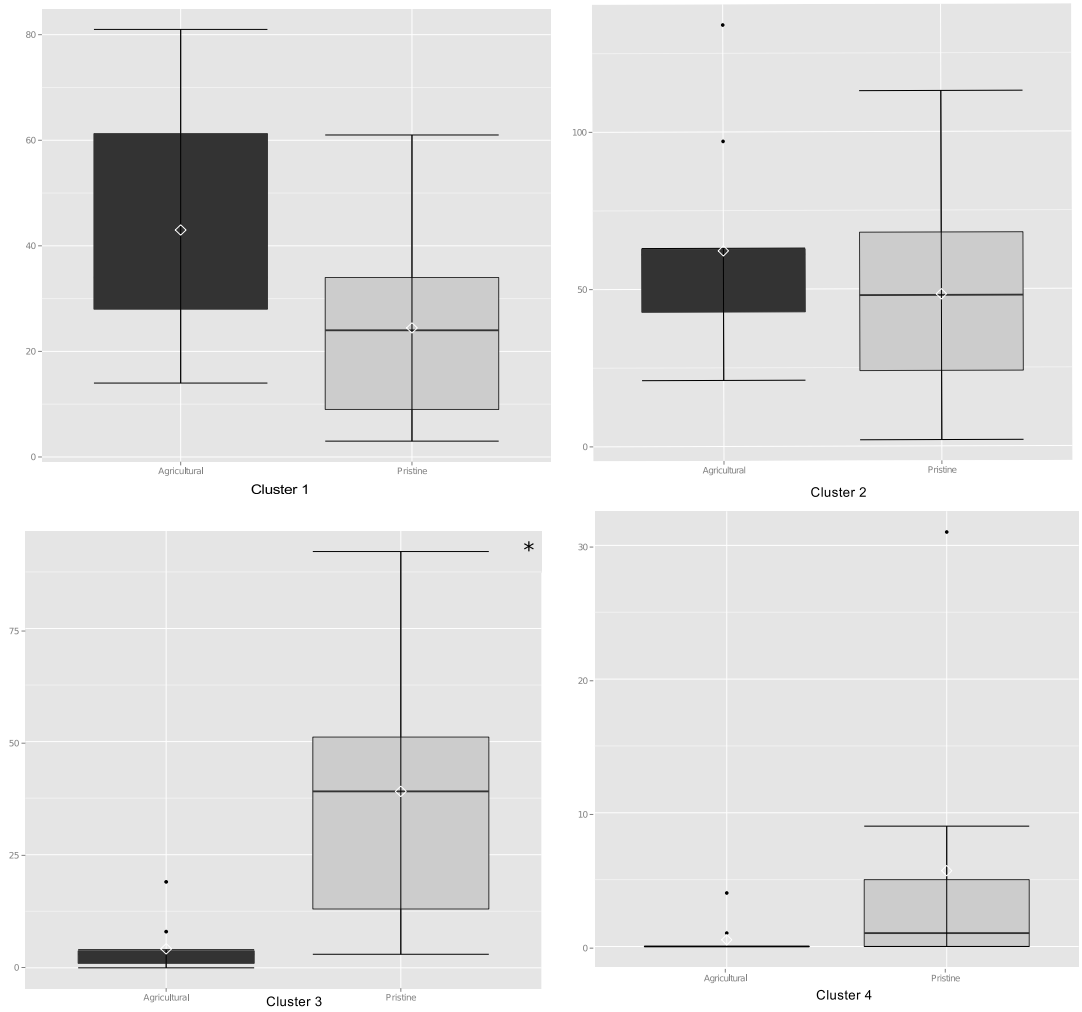

Figure 4.3. Relative abundances of the four functional clusters on agricultural and pristine areas Asterisk highlights significant differences between areas.

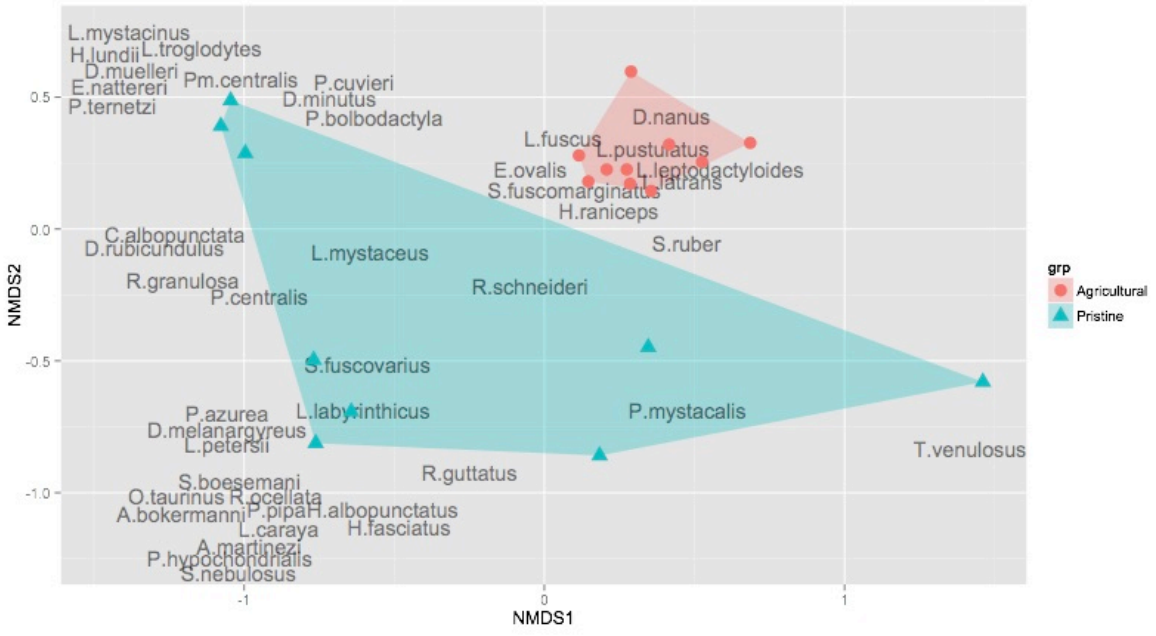

Figure 4.4. NMDS ordination of species by agricultural and pristine areas.

4.5.4. Null model validation

Observed functional richness in rice fields was significantly lower than null expectation 70% of the times. Faith's phylogenetic index is strongly affected by species richness. Observed mean phylogenetic distance in rice fields was significantly lower than randomly expected 80% of the times. Observed mean phylogenetic distance to the nearest taxon in rice fields was significantly lower than null expectation 70% of the times (Table 4.2). Hence, significant differences in functional and phylogenetic diversity metrics are not due to differences in species richness, but largely attributed to trait composition and community phylogenetic structure.

Table 4.2. Percentage of pristine and agricultural communities with an observed value of the functional or phylogenetic diversity measures significantly lower or higher than the null expectation ($P \leq 0.05$) with 999 simulations.

Index	Lower than null expectation (%)		Higher than null expectation (%)	
	Pristine Areas	Rice fields	Pristine areas	Rice fields
FRic	50	70	20	12
PDf	35	30	10	0
MPD	30	80	2	0
MNTD	66	70	0	3

4.5.5. Phylogenetic Diversity

PDf (t(9.43)=2.401, p= 0.03) and MPD (t(9.93) = 3.52, p=0.005) were significantly lower in rice fields than in pristine areas. MNTD (t(11.93) = 1.98, p=0.005) was significantly higher in rice fields than in pristine areas.

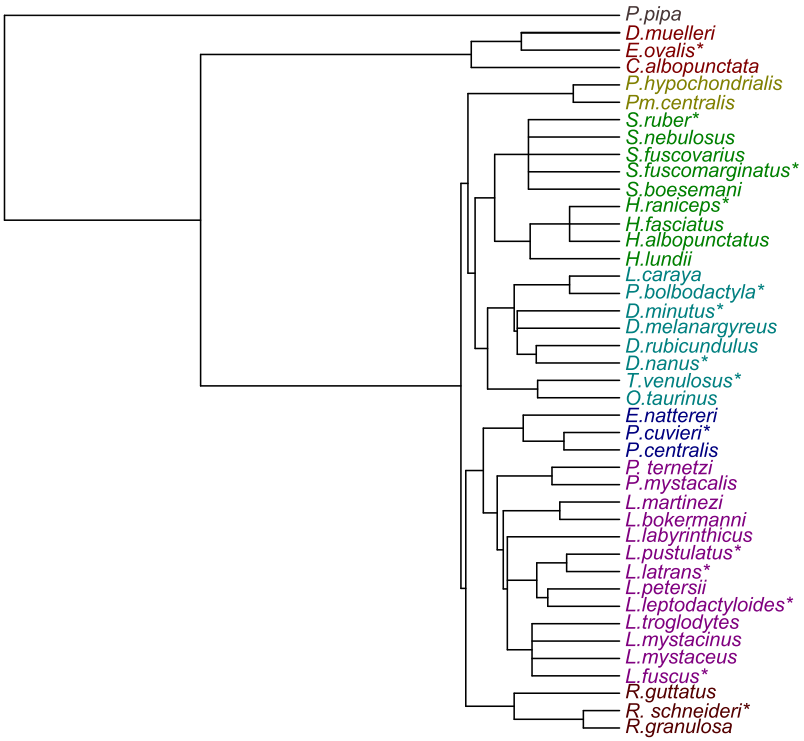

Figure 4.5. Phylogram with every species recorded during this study. Species with asterisks are those present in agricultural areas.

Of the seven clades that compose the total phylogeny, 2 are not represented in rice fields, 3

have ca. 30% of the clades represented in rice fields and 2 have approximately 50% of the clade represented in rice fields (Fig. 4.5).

4.5.6. Anuran trait association to agricultural landscapes

Our random forest models selected range size, SVL, clutch size and habitat as predictors of anuran species presence in rice fields. Our classification tree models identified two optimal trees for trait association with species presence in rice fields. In the first tree, small species ranges (< 599 km^2) determine species presence in crops, with 83% of the species with ranges smaller than 599 km^2 being absent from rice fields. In the second tree, anurans associated with forest and open area habitats have 77% probability of being absent from rice fields. If the described habitat association occurs in synergy with small clutch size (< 182 or 432), the probability of that species being absent from rice

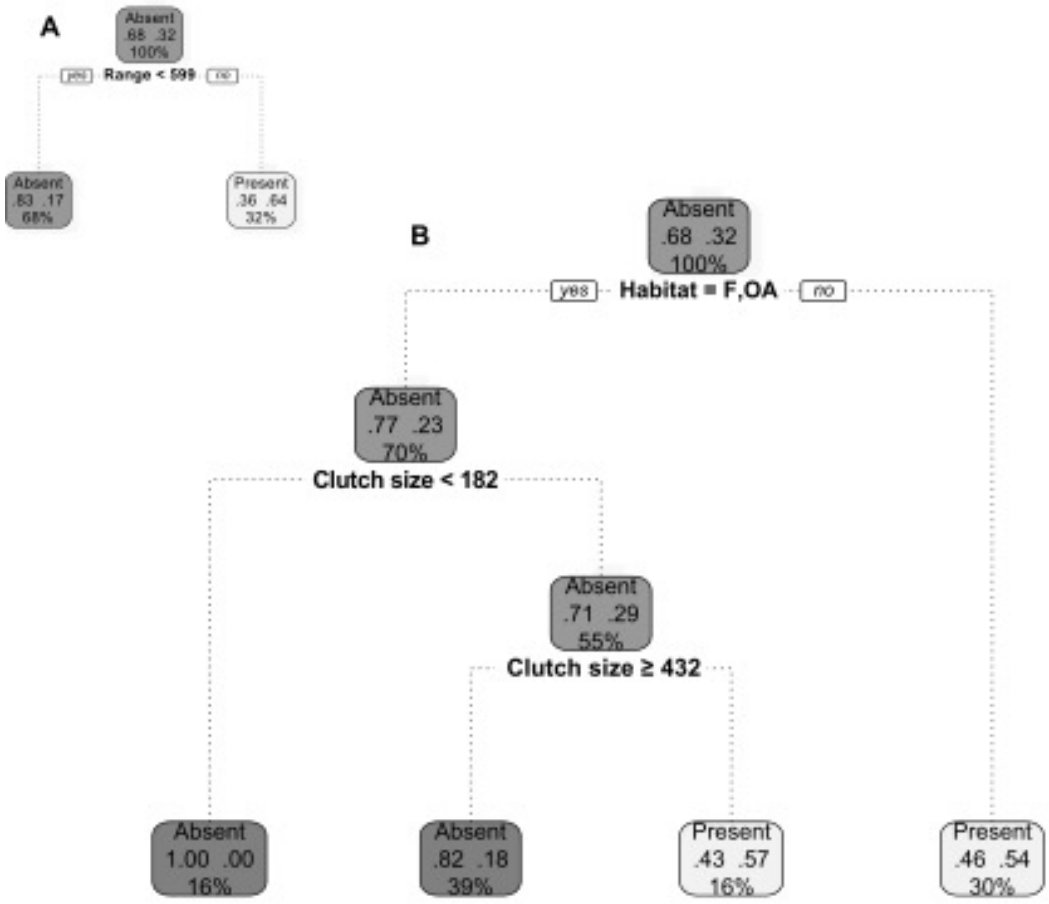

Figure 4.6. Classification tree models with the two optimal trees built for trait association to species presence in rice crops.

fields is high (100% or 82%). Anurans associated to forest or open area with larger clutches have a relatively high probability of occurring in rice fields (57%) (Fig. 4.6).

Our random forest models selected habitat, SVL, range size and clutch size as predictors of relative abundance of anuran species in rice fields. Our regression tree models identified three optimal trees for trait regression against species relative abundance in rice fields (Fig.4.8).

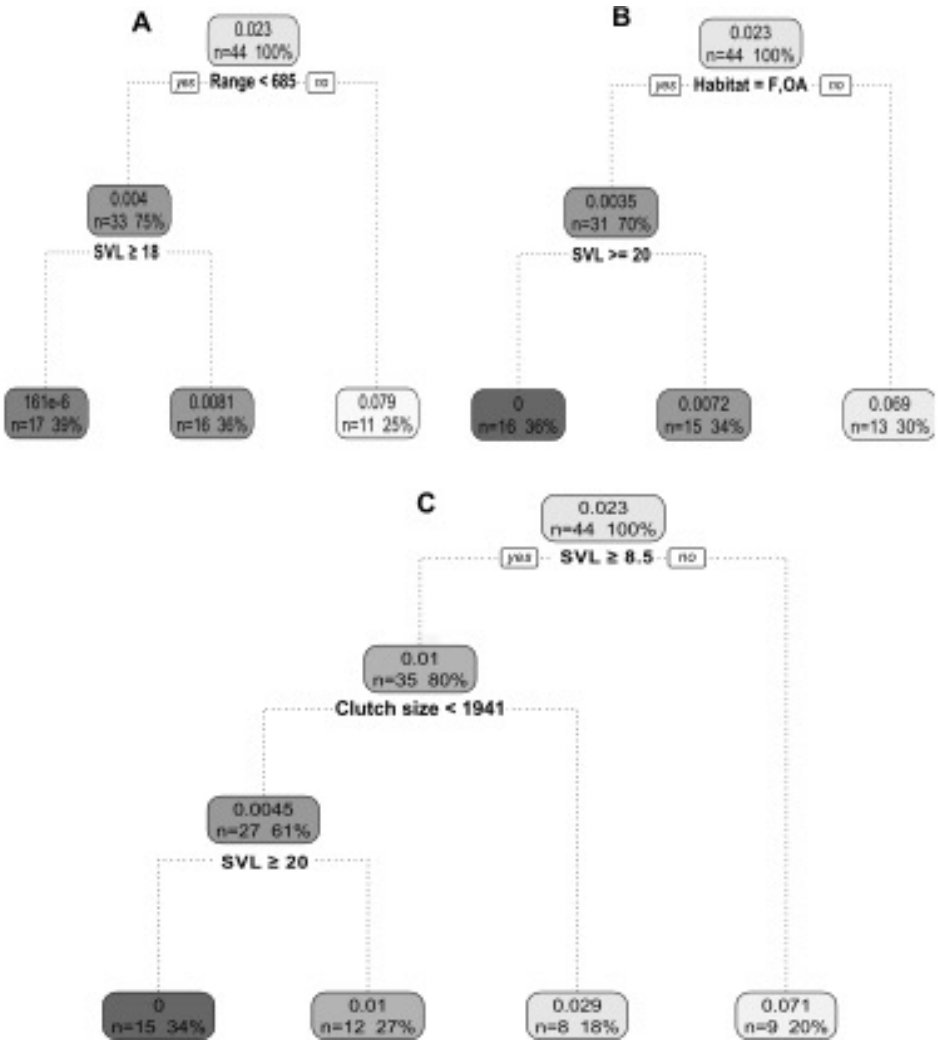

Figure 4.7. Regression tree models with the three optimal trees built for trait regression against species relative abundance in rice fields. A- First optimal tree; B- Second optimal tree; C- Third optimal tree.

In the first tree, small species ranges (< 685 km^2) results in low relative abundance in crops and, if in synergy with larger body size (≥ 18 mm), corresponds to a very low

relative abundance in rice fields. On the contrary, anurans with small ranges but smaller body size (< 18mm) are associated with relatively higher abundances in rice fields (Fig.4.7A). The second optimal tree identifies forest or open area habitat associations as determinant for low relative abundance in crops, which, if in synergy with larger body size, results in absence from crops (Fig.4.7B). The third optimal tree identifies larger body size and smaller clutches as determinant for low or null abundances in rice fields (Fig.4.7C).

4.5.7. Body condition index

Body condition indices for the genera *Dendropsophus* (D=0.9958, p=1.332e-15), *Hypsiboas* (D=0.9688, p= 2.864e-14) and *Leptodactylus* (D= 0.7622, p<2.2e-16) were significantly higher in pristine than in rice fields (Fig. 4.8).

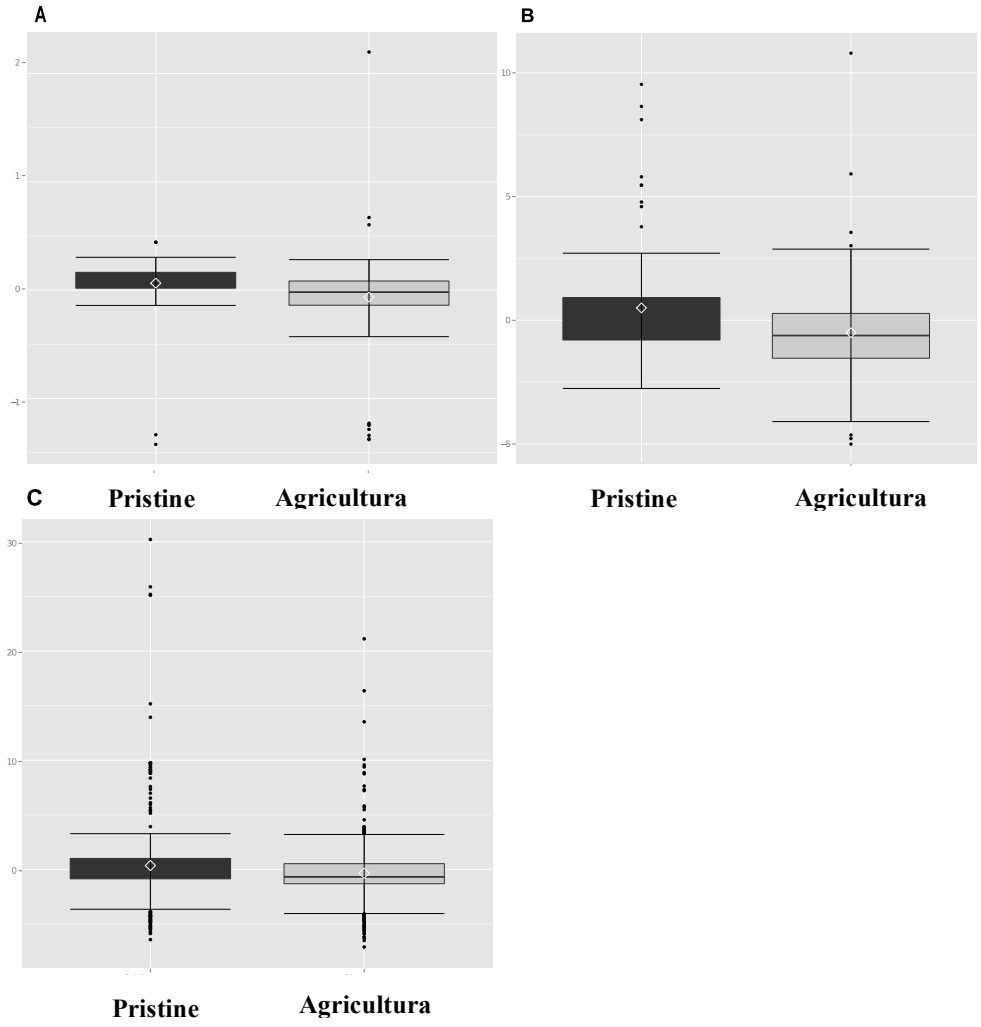

Figure 4.8. Body condition indexes for genus *Dendropsophus* (A), *Hypsiboas* (B) and *Leptodactylus* (C) in pristine areas and in rice fields.

4.6. Discussion

Our study is the first to integratively represent the effects of natural habitat conversion to rice fields on anuran communities. Habitat conversion and agricultural management have caused profound alterations to the anuran community, including dramatic loss of species diversity and functional richness and increased functional divergence. Community composition suffered severe alterations, resulting in dominance of generalist hylids and leptodactylids and low representation of specialist microhylids and bufonids. Anuran communities in rice fields exhibited decreased phylogenetic diversity and mean phylogenetic distance, and increased mean nearest phylogenetic distance, suggesting that anuran communities in agricultural areas are composed of phylogenetically related species and, therefore, are not as diverse as their pristine counterparts.

Taxonomic indices often show unimodal patterns, with higher species richness for intermediate disturbance levels and contribute to the misconception that disturbance may be advantageous to biodiversity. These indices are unable to accurately describe how disturbances affect biodiversity, unless other metrics are taken into consideration. Functional diversity indices are expected to decrease under high disturbance levels due to environmental filtering (Cornwell et al., 2006; Flynn et al., 2009), and are thus perceived as better translators of disturbance effects on communities and ecosystems. According to the performance filter hypothesis, the environment determines the performance of species according to their trait syndromes, posing environmental filters to communities and selecting trait combinations associated with increased fitness in the occurring conditions (Mouillot et al., 2013b). This means that even milder disturbances may deplete populations of species with vulnerable combinations of traits (e.g., habitat specialists) without modifying species composition and, thus, without affecting taxonomic indices. Functional and phylogenetic diversity indices provide deeper insights into the complex effects that disturbances have on biodiversity (Cornwell et al., 2006). Functional richness in particular has been invoked as a good predictor of ecosystem service because it describes species traits, translating the capacity of each species to provide a particular service (Díaz and Cabido, 2001). Indices based on both species traits and abundances, such as functional divergence or specialization, are more likely to act as

early-warning indicators as they do not need species extirpations or local extinctions to change (Villéger et al., 2010). Our study corroborates such conceptions because, although anuran species richness, functional richness and phylogenetic diversity were significantly lower in rice fields, taxonomic diversity did not vary significantly.

Phylogenetic diversity represents the total evolutionary history or phylogenetic relatedness of all species in a community (Faith, 1992), being recognized as intrinsically valuable for conservation (Winter et al., 2013). Several studies have suggested that communities with higher phylogenetic diversity are more stable (Cadotte et al., 2012), productive (Cadotte, 2013) and support more species (Dinnage et al., 2012). However, despite the known impacts of agriculture on species loss, the effects of habitat conversion on phylogenetic diversity remains largely unknown. Studies on plants and invertebrates suggest that environmental disturbances favor subsets of closely related clades, resulting in phylogenetic diversity loss (Helmus et al., 2010). Global extinction risk assessments of birds and mammals suggest that particular branches are at greater extinction risk than others (Verde Arregoitia et al., 2013). Although species richness was significantly decreased in rice fields, species loss alone did not account for declining phylogenetic diversity. The changes we detected in phylogenetic diversity result from species loss and increased species relatedness. Species in pristine areas were less related to one another than expected by chance, whereas species in rice were more closely related. These patterns indicate that anuran phylogenetic diversity loss in agriculture causes a shift in community composition while taxonomic diversity remains relatively stable.

Ecological resilience, the ability of ecosystems to absorb disturbances while maintaining key functions (Folke et al., 2004), is increasingly crucial considering global changes and increased human pressure on ecosystems. Ecosystem resilience safeguards vital services upon which humans and biodiversity depend, such as seed dispersal, pollination, and pest control (Foley et al., 2005). Functional richness and redundancy are important aspects of ecosystems resilience (Allen et al., 2005). While FRic describes the diversity and range of functional traits responsible for ecosystem services (Wright et al., 2006), functional redundancy represents the number of species fulfilling the same function. Ecosystems are more resilient when a given function is fulfilled by multiple species, which minimizes the

probability of trait extinction. In highly functionally redundant communities, if one species goes extinct, others will continue to fulfill the same functions and ensure community functioning even under increasing pressure, allowing long-term sustainability of ecosystems and their services (Tscharntke et al. 2005). Amphibians play keystone roles in ecosystem functioning; in food webs, they act as both predators on invertebrates and small vertebrates and as prey for larger animals, and they establish an avenue for nutrient transport between aquatic and terrestrial systems. Loss of amphibian functional richness and an increase in functional divergence may affect vital ecosystem processes and contribute to loss of system resilience and resistance (Davic and Welsh, 2004).

The dramatic decline in FRic and the increase in functional divergence following conversion of natural habitats to rice fields indicates that the loss of more sensitive species is not counterbalanced by the addition of new, disturbance-tolerant species that could either fill vacant functional niches or occupy different functional roles. Anuran communities from rice fields were strongly dominated by a few generalist species (e.g., *D. nanus*, *L. latrans*), while communities from pristine areas were composed by more species, many specialists, occurring at lower abundances. These community changes provide strong evidence for environmental filtering in agricultural landscapes. Generalists with short life cycles and high reproductive capacities (i.e. r-selected species, Begon et al., 1996) are favored, and K-selected specialists are excluded from the communities due to lower ability to adapt to the fluctuating resources of intensively managed agricultural lands (Begon et al., 1996). While habitat loss and pesticide burden are important drivers of extinction of specialized and rare species, habitat fragmentation per se and the disrupted exchange of individuals between local communities affect less mobile species. Reduced dispersal affects meta-population dynamics, resulting in increased extinction risk for less vagile species (Schweiger et al. 2005). Consequently, intensively cultivated landscapes will be dominated by generalist and mobile species. Functional groups composed mainly of specialized, rare, or less mobile species have higher extinction risk when land use is intensified than groups dominated by generalist or highly mobile species (Schweiger et al., 2007).

Small geographic ranges, association with forest and open area habitats, small clutches and large body size are associated with low to null species abundances in rice fields. Indeed,

while pristine communities were composed of many, similarly abundant species, with varied degrees of habitat specialization, clutch and body size, agricultural communities were composed of few widespread habitat generalists, with smaller body size and larger clutches, such as *D. nanus* or *L. latrans*. Large body size and small range are the most common predictors of high extinction risk for several organisms (Botts et al., 2013; Gilroy et al., 2014; Sodhi et al., 2008). The most consistently significant correlate with amphibian decline risk is geographic range size (Botts et al., 2013). Small-range species are more likely to decline, become threatened and eventually suffer extinction (Devictor et al. 2010; Murray et al. 2011; Sodhi et al. 2008). Species with small ranges are often less abundant, less mobile, poorer competitors and have lower reproductive success than more widespread species (Cooper et al., 2008; Sodhi et al., 2008). The geographic area of a species depends on suitable environmental conditions, ability to disperse and to successfully compete with other species and survive predation (Olalla-Tárraga et al., 2011). Species with large ranges often tolerate a wide variety of conditions, while species with small ranges are only able to persist under a narrower range of conditions. Hence, the size of a species range is, at least partially, a spatial representation of its degree of specialization (Cooper et al., 2008; Devictor et al., 2010; Sodhi et al., 2008). Strong association with forest and open area habitats are also correlated with higher degrees of specialization. The anurofauna of the Cerrado is composed of species strongly associated with forest formations, those dependent on open area formations and those that are widespread generalists (Valdujo et al., 2012). Forest associated species have specialized breeding strategies, such as terrestrial clutches and lotic tadpoles, while open area specialists often produce foam nests in subterranean chambers to minimize humidity loss and temperature fluctuation. Larger body sizes generally correlate with slower life history traits, thus decreasing recovery potential after population crashes (Sodhi et al., 2008). Anuran body size reflects effects of reduced surface to volume ratios in larger species to control both heat and water balance (Olalla-Tárraga et al. 2009); thus, larger species are commonly associated with high water deficit areas, whereas smaller species are usually found in humid areas. In addition, assuming resistance to desiccation relates to mobility, larger species forced to migrate across agricultural matrices, from shelter areas to breeding areas, might be more successful than smaller ones. Our results indicate that agricultural activities such as pesticide application and

ploughing may be significantly more detrimental to larger species and may offset the physiological advantage that larger body size has in regulating body temperature and increasing mobility. Small clutches are correlated with decreased survival probabilities, especially in unstable and adverse conditions, such as those present in agricultural environments.

Most studies on the effects of agricultural activities on amphibians are based on abundance or density changes. While these metrics are useful, less conspicuous effects occur at the individual and population level. Although the effects of habitat change on body condition are seldom studied, the few studies available indicate that anurans in agricultural areas have lower body condition than their pristine counterparts (e.g. Brodeur et al. 2011; Karraker and Welsh 2006; Neckel-oliveira 2007). Body condition indices are surrogates for the animal's mass associated with energy reserves after correcting for structural body size. An individual in good condition is assumed to have more energy reserves than an animal in poor condition. As energy stores can be allocated for maintenance, growth or reproduction, animals with larger energy reserves will usually have better fasting endurance, survival and reproductive output than individuals with smaller reserves (e.g., Bachman and Widemo 1999). Consequently, the lower body condition observed in frogs from cultivated sites is an indication that these animals have reduced fitness and suggests that ecologically relevant parameters such as reproductive output and survival may be impaired in these populations (Brodeur et al., 2011). Higher abundance of generalists in agricultural areas may result in increased competition for resources and in lower body condition. High exposure to fertilizers and pesticides in crops may stimulate the organism's compensation/detoxification systems to re-establish homeostasis, explaining the reduction of energy reserves due to physiological alterations and consequent increase of energetic maintenance costs. Another explanation for the reduced body condition of frogs from agricultural areas would be for food intake to be lower in cultivated sites due to either the smaller area of habitat available or to a decrease in the abundance of prey insects caused by insecticide applications. Our results highlight the need for further investigations into the causes and consequences of the low body conditions consistently found in anuran communities from agricultural environments.

Understanding how species traits correlate with their responses to agriculture will allow better predictions of the functional effects of anthropogenic land-use (Newbold et al., 2013). Diversity itself is an important component of ecosystem resilience because diverse communities are more likely to hold multiple species capable of contributing to a single given function. Our results show that the conversion of natural Cerrado-Amazon vegetation to vast rice fields results in such environmental stresses, that large subsets of species are driven to local extinction irrespective of their specialization. Species commonly perceived as resilient to habitat alteration did not occur in these environments (e.g. *Leptodactylus labyrinthicus*, Heyer 2005), which indicates that the new environmental filters, arisen as a consequence of replacing native vegetation with rice fields, are more detrimental on Neotropical anurans than was expected. Our results corroborate previous studies (e.g., Cooper et al. 2008; Hero, Williams, and Magnusson 2005; Lips, Reeve, and Witters 2003; Murray and Hose 2005) but also deliver new insights into potential synergies of different drivers of anuran community change in agricultural environments. This study supports previous findings that traditional metrics such as taxonomic diversity can hide important information about the real impacts of anthropogenic land-use on species composition and ecosystem functioning. Integrative approaches provide holistic insights on the impacts and consequences of human-mediated disturbances on biodiversity, potentially contributing to future conservation and agricultural management decisions (Hidasi-Neto et al., 2012; Vandewalle et al., 2010).

4.7. References

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Supplementary material

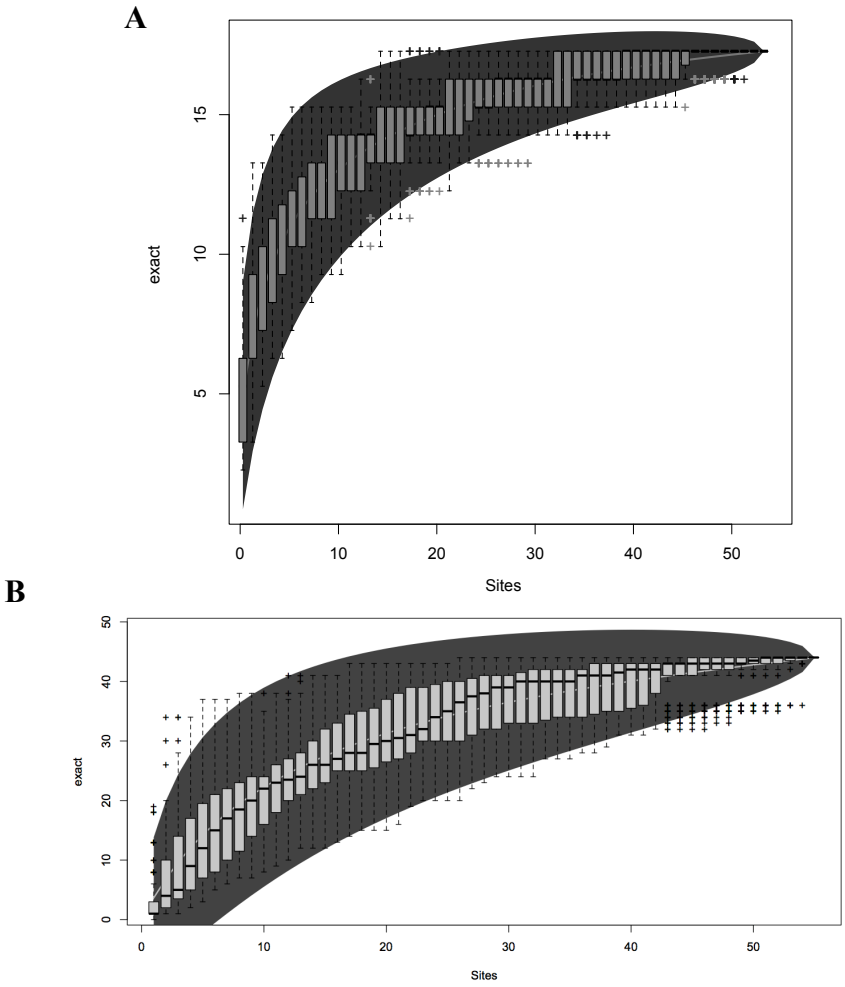

Figure A4.1. Species accumulation curve for agricultural (A) and pristine (B) environments, with chao1 estimator standard errors represented.

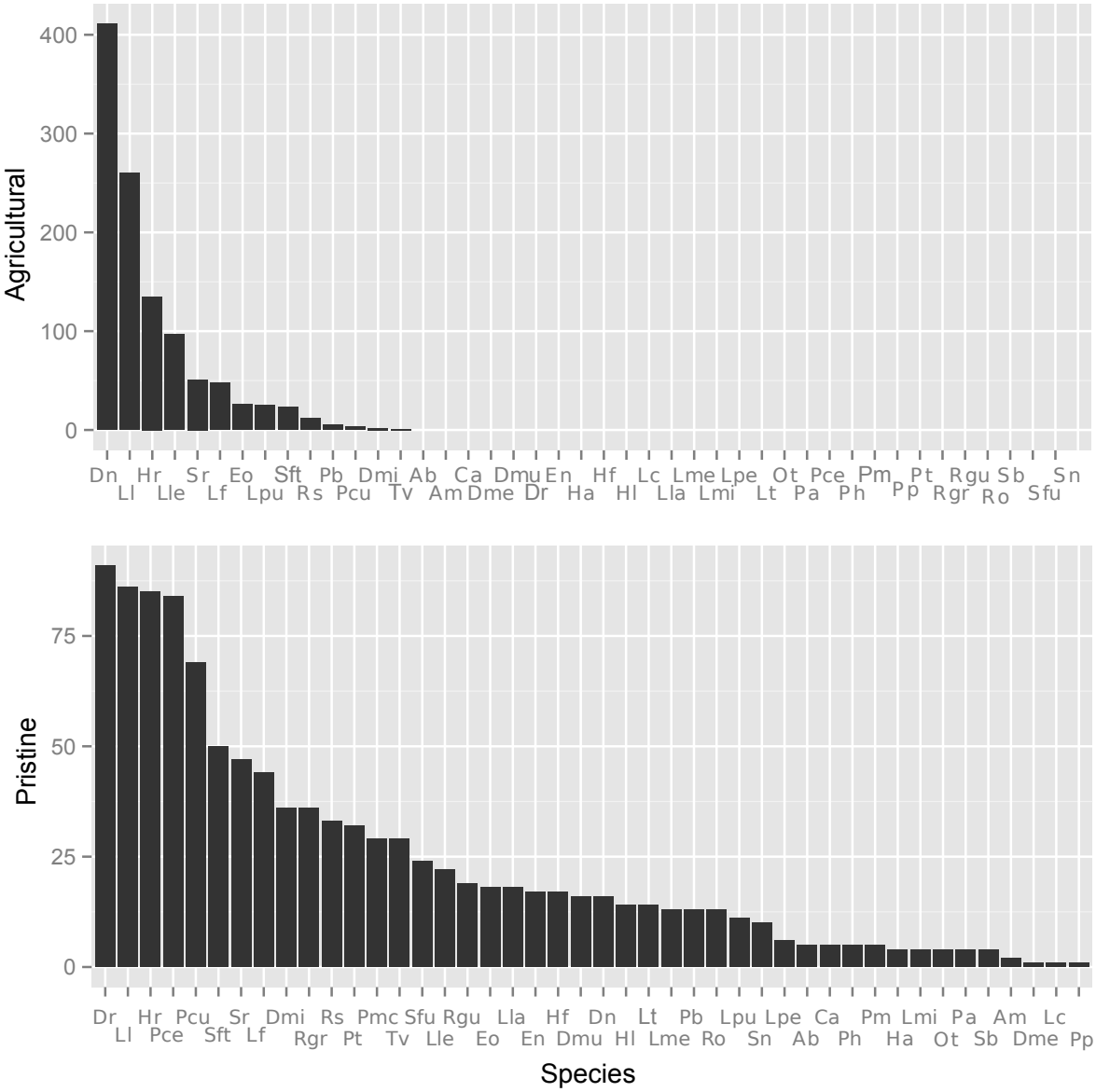

Figure A4.2. Species abundance in agricultural and pristine areas. Dn: *Dendropsophus nanus*; Ll: *Leptodactylus latrans*; Hr: *Hypsiboas raniceps*; Lle: *Leptodactylus leptodactiloydes*; Sr: *Scinax ruber*; Lf: *Leptodactylus fuscus*; Eo: *Elachistocleis ovalis*; Lpu: *Leptodactylus pustulatus*; Sft: *Scinax fuscomarginatus*; Rs: *Rhinella schneideri*; Pb: *Pseudis bolbodactyla*; Pcu: *Physalaemus cuvieri*; Dmi: *Dendropsophus minutus*; Tv: *Trachycephalus venulosus*; Ab: *Adenomera bokermanni*; Am: *Adenomera martinezi*; Ca: *Chiasmocleis albopunctata*; Dme: *Dermatonotus muelleri*; Dmu: *Dendropsophus melanargyreus*; Dr: *Dendropsophus rubicundulus*; En: *Eupemphix nattereri*; Ha: *Hypsiboas albopunctatus*; Hf: *Hypsiboas fasciatus*; Hl: *Hypsiboas lundii*; Lc: *Lysapsus caraya*; Lla*: Leptodactylus labyrinthicus*; Lme: *Leptodactylus mystaceus*; Lma: *Leptodactylus mystacinus*; Lpe: *Leptodactylus petersii*; Lt: *Leptodactylus troglodytes*; Ot: *Osteocephalus taurinus*; Pa: *Phyllomedusa azurea*; Pce: *Physalaemus centralis*; Ph: *Phyllomedusa hypochondrialis*; Pm: *Pseudopaludicola mystacalis*; Pp: *Pipa pipa*; Pt: *Pseudopaludicola ternetzi*; Rgr: *Rhinella granulosa*; Rgu: *Rhaebo guttatus*; Ro: *Rhinella occelata*; Sb: *Scinax boesemani*; Sfu: *Scinax fuscovarius*; Sn: *Scinax nebulosus*.

"-Sí, al borde del vacío comprendió lo más importante - maulló Zorbas.

-Ah, sí? Y qué es lo que comprendió -preguntó el humano.

-Que sólo vuela el que se atreve a hacerlo - maulló Zorbas."

Luis Sepúlveda, *Historia de una Gaviota y el Gato que no Sabía Volar*

Chapter 5

Landscape and local correlates of anuran taxonomic, functional and phylogenetic diversity in rice crops.

5. LANDSCAPE AND LOCAL CORRELATES OF ANURAN TAXONOMIC, FUNCTIONAL AND PHYLOGENETIC DIVERSITY IN RICE CROPS.

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5.1. Abstract

Deforestation is a major driver of biodiversity loss, mainly due to agriculture. As rice is among the world's most important crops, determining how agricultural communities are shaped is imperative. However, few studies have addressed the factors that alter community assembly in human-modified landscapes. We aim to quantify taxonomic, functional, trait and phylogenetic diversity of an anuran community from rice crops on a biodiversity hotspot. Identify local and landscape characteris- tics responsible for variations in multiple dimensions of anuran diversity in rice crops. This study was performed in Tocantins, Brazil. We chose 36 lentic waterbodies on rice fields for anuran sampling. We quantified taxonomic diversity (TD), functional diversity (FD) and phylogenetic diversity (PD) for each waterbody. We also estimated the mean functional differences among species for each trait separately. To evaluate how local and landscape scale features affect anurans, we performed generalized linear mixed models in 500, 1000 and 1500 m buffers around each waterbody. We found increased PD and FD in water- bodies closer to many other waterbodies and large forest patches. Anuran biomass decreased with increasing distance to the closest waterbody. Trait diversity varied with waterbody abundance and closeness, percentage of bare ground and marginal vegetation. Our study emphasizes the importance of waterbody and forest patch networks for maintain- ing high anuran FD and PD in agricultural landscapes. As both metrics are known to be related to ecosystem resilience, understanding these patterns is pivotal for

biodiversity management, especially in the tropics, where agricultural expansion is unrelenting and biodiversity is especially unique.

Keywords: Neotropics; agriculture; amphibians; traits.

5.2. Introduction

Deforestation is a major driver of biodiversity loss, especially in the megadiverse Neotropics, where it is mainly caused by agricultural expansion (Garcia-Barrios et al. 2009). Anthropogenic activities such as agriculture and cattle farming are known to cause profound and complex alterations to communities and ecosystems (Williams-Guillen and Perfecto 2010; Frishkoff et al. 2014). Rice is the world's most important food crop, occupying 11% of the world's total arable land (Kang and Priyadarshan, 2007). Asian countries are responsible for 90% of the world's production, while Latin America and the Caribbean produce 4.1%, half of which comes solely from Brazil (FAO, 2011). Several studies have reported negative effects of habitat conversion to irrigated rice crops on biodiversity (e.g. Attademo et al. 2011; Hyne et al. 2009; Maximiliano Attademo et al. 2015). However, these agricultural wetlands have also been considered valuable for birds and amphibians (Czech and Parsons 2002; Elphick and Oring 2003; Bambaradeniya and Amarasinghe 2004; Leps et al. 2006) and even functional equivalents to natural wetlands. (Bambaradeniya and Amarasinghe 2004). Given the extension and location of rice fields worldwide, determining how communities living in these environments are shaped is of the utmost concern, especially in the tropics, where rice production meets important social and economic demands, and biodiversity is especially high and unique.

Wetlands are important breeding habitats for many amphibian species and irrigated rice fields are invariably used by local amphibians to forage and reproduce. Due to their generally biphasic life cycle, highly permeable skin and ectothermic physiology, amphibians are very dependent on environmental quality and vulnerable to its change (Niemi and McDonald 2004). These characteristics have made amphibians the most threatened vertebrates worldwide, especially due to habitat destruction (Stuart, 2004). They play keystone roles in ecosystem functioning, acting as both predators and prey, enable nutrient transport between aquatic and terrestrial systems and are among the most diverse and abundant vertebrates, comprising species from a variety of habits, breeding strategies and dispersal abilities. Loss of amphibian species may therefore affect vital ecosystem processes and contribute to loss of system resilience and resistance (Davie and Welsh 2004). Due to their ecological importance and sensitivity, amphibians constitute

reliable surrogates to evaluate the effects of human disturbances on whole communities and ecosystems (Davie and Welsh 2004).

Although some studies have already investigated the variables that affect community composition in anthropogenic landscapes, most were based on taxonomic metrics (Sodhi and Ehrlich 2010), leaving important community and ecosystem-level consequences unaddressed. Species richness relies on the assumption that all species are equal, i.e., only relative abundances determine the importance of species in communities 15 and ecosystems (Magurran 2004). However, some species are more distinct from an evolutionary perspective or carry functional traits especially important for ecosystem processes than others (Cadotte et al. 2010; Mouillot et al. 2013). As the effects of anthropogenic environmental alteration on species are ultimately mediated by traits (e.g. physiological constraints, habitat preference, dispersal ability), considering only taxonomic metrics may fail to provide accurate conclusions on the real consequences of anthropization on biodiversity.

Landscape modification often creates new environmental filters that favor particular attributes for species persistence, generating generalist communities with species richness similar and sometimes even higher than pristine environments. In order to attain more representative conclusions on the effects human activities have on communities, we must account for different components of biodiversity, such as functional (FD) and phylogenetic (PD) diversity.

FD describes the variability in ecological attributes among species, being often considered representative of ecosystem resistance, resilience and functioning (Petchey and Gaston 2006). Measuring FD is equivalent to measuring functional trait diversity, where functional traits are components of an organism's phenotype that influence ecosystem processes. PD analyzes the evolutionary differences between species (Faith, 1992), representing an estimate of phylogenetically conserved ecological and phenotypic differences between species (Cavender-Bares et al. 2009). This metric may characterize the evolutionary potential of biodiversity to respond to environments (Cisneros, Fagan, and Willig 2014). Studies approaching the effects anthropogenic landscapes have on species traits, FD or PD (Tscharntke et al. 2012) are still scarce but, while most focused

on plant and invertebrate assemblages (e.g., Arroyo-Rodríguez et al. 2012; Aviron et al. 2005; Laliberte et al. 2010), others have successfully explored the effects human activities have on vertebrate communities (e.g. Ernst et al. 2006, Trimble and Aarde 2014). However, the influences of landscape and local features of agricultural landscapes on communities are seldom investigated (but see Cisneros et al., 2014).

Human-mediated landscape modification is spatially complex, as native formations are fragmented and replaced by a variety of anthropogenic land cover types. These new landscape matrices are not completely inhospitable to biota, and species dispersal ability and plasticity in resource use often determine its ability to endure in these environments (Kupfer et al., 2006; Perfecto & Vandermeer, 2008).

Land cover change alters resource availability and diversity, as well as connectivity among resource patches. Landscape modification has three main consequences for the fauna: loss of native vegetation; fragmentation and alteration of matrix permeability (Tscharntke et al., 2012). Because species are affected in multi-dimensional manners (e.g. landscape composition and configuration), understanding the effects of native vegetation loss, fragmentation, and matrix configuration on community assembly requires considering multiple scale-dependent compositional and configurational landscape features.

We aim to quantify taxonomic, functional, trait and phylogenetic diversity of an anuran community from rice crops in a Neotropical biodiversity hotspot. Our objective was to identify local and landscape characteristics responsible for variations in multiple dimensions of anuran diversity. To our knowledge, this is the first study to assess the effects that landscape and local features of agricultural systems have on taxonomic, functional, trait and phylogenetic diversity of a Neotropical anuran community.

5.3. Methods

5.3.1. Study area and sampling design

This study took place in an ecotone region between the Amazon rainforest and the Brazilian savanna, the Cerrado, in the municipal district of Lagoa da Confusão, state of Tocantins, Brazil. Agricultural landscapes of this area are characterized by the presence

of *ipucas*, "islands" of closed native vegetation which remain flooded longer than the surrounding areas. These landscapes are composed of vast crop areas speckled by many "islands" of native vegetation of variable dimensions. The region is a seasonally flooded area, with a very pronounced rainy season from October to April.

Irrigated rice fields in the Cerrado-Amazon ecotone present a dynamic hydrologic regime, with variation between aquatic and terrestrial phases. When rice is being grown, from December to April, rice fields remain with surface water until harvest, before which crops are completely drained. After rice harvesting, crops may remain fallow or other crops may be cultivated, depending on the landowner's will. Besides rice fields, the region's landscape is also occupied by pasture areas, where cows, emus or water buffalos roam. This area has been under agricultural exploration for the last 30 years, especially targeting rice production. Given the temporal extent of this exploration, we consider these communities as stable, despite the use of pesticides and crop management procedures.

We chose a total of 10 rice fields along the Rio Formoso irrigation project (Fig. 5.1). Rice fields varied in size, *ipuca* and waterbody abundance and size. We selected 4 to 5 temporary lentic waterbodies for anuran sampling in each rice field, totalizing 35 waterbodies. In order to investigate how local and landscape characteristics affect anuran diversity in rice crops, sampled waterbodies were chosen to represented the variance in habitat and landscape-level characteristics present in rice crop waterbodies. Due to logistic constraints, average accessibility to the waterbodies was also considered, as difficulty to sample was an important constraint for some waterbodies. We chose small (25 m^2) to large (1200 m^2) waterbodies. All waterbodies were located inside the agricultural matrix or less than 50 m from rice crops. All waterbodies were at least 450 m apart, and the maximum distance between waterbodies was 7km.

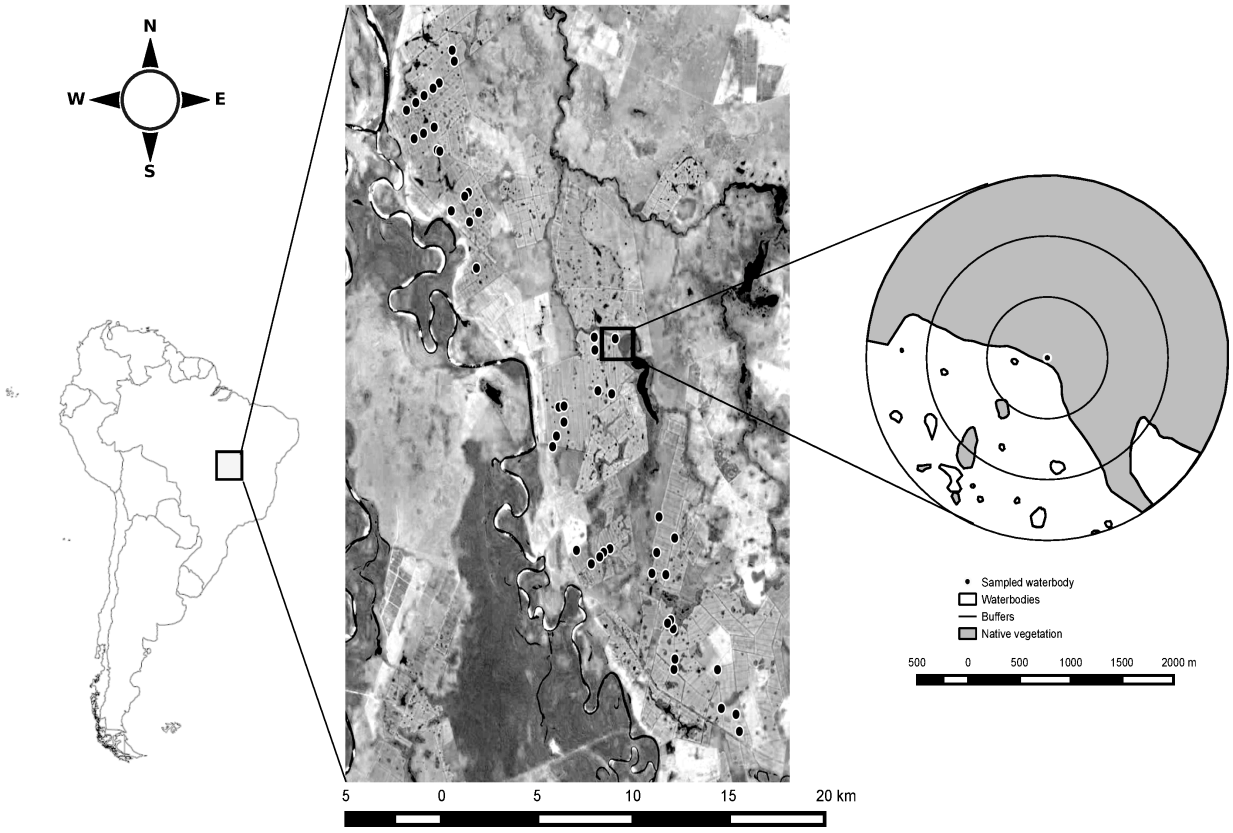

Figure 5.1. Study area and design. Dark circles represent the waterbodies sampled. Diagram showing the design of the 500m, 1000m and 1500m buffers we considered to evaluate the influences of landscape features and anuran diversity.

5.3.2. Anuran surveys

Agricultural surveys were conducted during two rainy seasons, from February 2013 to April 2014. Anuran sampling was performed using nocturnal visual encounter surveys along the 10 m wide margin of each waterbody, for approximately 30 min. Every individual seen perched on the vegetation, on the floor, under the leaf litter, logs or stones was caught, identified, measured, weighed, photographed and then released near the site of origin.

5.3.3. Local waterbodies characteristics

Environmental variables such as percentage of bare ground, herbaceous vegetation, shrubs, trees, shaded ground, leaf litter, logs/rocks, aquatic vegetation, herbaceous vegetation height, shrub vegetation height, herbaceous vegetation heterogeneity and shrub vegetation heterogeneity were registered. These variables were quantified performing transects (10 m long x 1 m wide) set on the sampled waterbody margin. For every meter, a 50 cm x 50 cm grid would be placed above the ground and the number of squares with 50% or more coverage of each variable would be summed and divided by the total (25 squares).

5.3.4. Landscape features

We quantified landscape features on the vicinity of each waterbody using high resolution Google Earth satellite imagery representing the landscape of the year 2014, on which we could easily discern crops from natural vegetation. This satellite classification was afterwards corroborated through presential visits to the main features on the field. For each of the 36 sampled waterbodies, we quantified distance to the closest waterbody, distance to the closest forest patch and number of waterbodies, number of forest patches, total waterbody area, total forest area, mean forest patch area and mean waterbody area within 500 m, 1000 m and 1500 m buffers (Fig. 5.1). While compositional features, such as number of forest patches or total waterbody area describe the proportions of different types of land use within the area surrounding a waterbody, configurational features, such as distance to the closest forest patch or waterbody, specify the geometric arrangement of land features surrounding a waterbody. Both compositional and configurational features were considered based on the acknowledged importance of such features for amphibian breeding success, migration and, consequently, metapopulation sustenance (Dodd, 2009). Trying to cover every possible function these features might have for the anuran community, we decided to consider multiple variables, despite their high apparent correlation. For example, while mean forest patch size and number of forest patches are correlated, they address different perspectives; mean forest patch size is important for addressing species which mostly exist within those environments, while number of forest

patches addresses the stepping stone character of each forest patch, and therefore, is relevant to species that use forest patches in dispersion.

Because spatial patterns are scale dependent, and anuran communities from anthropogenic environments are affected by different features on different scales, the scale at which anurans react to the environment differs among species, depending on a series of traits (Gorresen et al., 2005; Klingbeil & Willig, 2009). We quantified landscape characteristics at three spatial scales (buffers of 500, 1000 and 1500 m radius) that we found significant for amphibians regarding known dispersal abilities, to account for interspecific differences in anuran dispersal and ability to endure in agricultural systems.

5.3.5. *Anuran Data*

We compiled life history and ecological traits for every anuran species registered in the agricultural and pristine study areas. For each species we compiled information of 12 traits: activity, habits, habitat, fossorial behavior, adult snout-vent length (SVL), breeding site, breeding strategy, clutch size, parental care, breeding season, breeding pattern and geographic range size. We chose these traits based on perceived importance for determining species resilience to agricultural activities (Table A1) and on data availability. We compiled trait data from the literature, the AmphibiaWeb and IUCN online databases. If published data were unavailable, we relied on expert opinion or inferred trait information based on closely related species. Because breeding site, breeding season and breeding pattern were very homogeneous along the agricultural anuran community, we decided to exclude these three traits from the following analyses.

We used the phylogenetic tree built by Isaac et al. (2012) from the amphibian 'tree of life' described by Faivovich et al. (2006), with 5713 amphibian species and respective branch lengths. We pruned this supertree to build a smaller phylogenetic tree with every species sampled in rice crops. All operations related to pruning the original Isaac et al. (2012) supertree were performed using package Ape (Paradis et al. 2004) in program R.

5.3.6. Biodiversity metrics

At each site we quantified TD using Simpson's diversity index (Simpson, 1949), and FD and PD through Rao's quadratic entropy (Botta-Duke at, 2005). As Rao's Q derives from Simpson's index, hence including information on species differences, it can be used for the three dimensions (TD, FD and PD), which facilitates the comparison among different metrics. Rao's Q corresponds to the sum of functional or phylogenetic distances among all species, weighted by the product of their abundances, hence describing the abundance-weighted average difference between species from a community (Weiher, 2011).

Rao's Q, is commonly used in a multi-trait perspective, however, due to its intrinsic versatility, it can also be used to translate variability in trait state, e.g. regarding habits, how many different habits are in the space we are studying. Given the amount of trait information we collected for this community, we decided to explore how rice crops affected variability in trait state, and go beyond FD, which measures overall functional trait diversity. Hence, because landscape and local agricultural features may affect particular traits differently, we estimated the mean functional differences among species for each trait separately (e.g., habitat, breeding mode), as well as for all traits combined, corresponding to the FD metric. We obtained functional and phylogenetic distances between species from pairwise dissimilarity matrices for each trait separately, for all traits combined, and for the phylogeny. We built functional pairwise dissimilarity matrices using the Gower distance matrix, which quantifies dissimilarities with categorical and numeric attributes simultaneously (Botta-Duké at, 2005). In order to compare dimensions, we transformed each metric into its effective number of species (Jost, 2006), allowing direct interpretation of differences among indices (Jost, 2006). We calculated FD with function dfFD from package FD, and PD and TD with function raoD from package picante on program R.

We also determined anuran biomass directly, through the total anuran weight collected in each waterbody, and tested how it was affected by the considered predictors.

5.3.7. Phylogenetic signal

To facilitate ecological interpretation of phylogenetic patterns, we used abouheif's Cmean test to measure the strength of phylogenetic signal of the traits we used. Abouheif's Cmean tests the statistical dependence between species' traits due to phylogenetic affinities, using Revell et al. (2008) both categorical and mensural attributes. This approach evaluates if traits on a phylogeny are overdispersed, independent, consistent with a model of Brownian motion or conserved. If trait distribution along a phylogeny is consistent with a model of Brownian motion or conserved, traits exhibit phylogenetic signal and phylogenetic patterns can be interpreted with regard to those traits. Abouheif's Cmean test of phylogenetic signal was calculated with the R package adephylo (Jombart & Dray, 2010).

5.3.8. Quantitative analyses

We performed principal component analysis on waterbody characteristics, in order to assess local variable importance for overall variance and inter-variable correlation. We used package FactoMineR (Lê et al. 2008).

We performed generalized linear mixed models (GLMMs) to examine the effects of local and landscape features on anuran biomass and taxonomic, phylogenetic, functional and trait diversity. Because the 1000 and 1500 m buffers used to characterize the surroundings of each waterbody included other waterbodies within the same rice field, we used rice field as random effect. Random effects are especially useful for inferring on a population when the data available are random samples of that population, assuming it is a meta-population, and that our sample reflects many draws from that population. So rather than anchoring results around heterogeneous intercepts, the data will be used to elucidate the parameters of that distribution from which data were drawn.

Model fit for each dependent variable was manually assessed from the null model, to avoid automatic variable elimination for the sake of model fit optimization only. We choose to assess model fit and predictor significance through F-tests performed among nested models por each dependent variable (FD, PD, TD, each trait's diversity and Biomass), first progressively evaluating each predictor's significance, then fitting

reduced models with the most significant predictors, and finally assessing the reduced models' fit against the full model, using F tests. We fit all models using the lme4 package (Bates 2007).

We performed hierarchical partitioning (HP) to further determine the relative independent importance of each significant variable. We determined the statistical significance of each independent variable's independent contribution using a randomization approach with 5000 iterations and an alpha- level of 0.05 (Mac Nally, 2002). We executed hierarchical partitioning using package 'hier.part' (Mac Nally & Walsh, 2004).

5.4. Results

Relationships between landscape and local characteristics and anuran diversity were scale and metric-specific (Table 5.1). TD variation across waterbodies was affected mainly by local waterbody and landscape characteristics ($F_{(8, 26)} = 14.78$, $p = 0.048$, Table 1). TD decreased 67% with increased percentage of terrestrial leaf-litter (Fig. 5.2E), and with increased mean forest patch area within the 500 m buffer (Fig. 5.2D).

Variation in PD was mainly accounted for by the number of forest patches within the 1500 m buffer ($F_{(9, 26)} = 20.34$, $p = 0.034$); increased number of forest patches was associated to a 92% increase in phylogenetic diversity (Fig. 5.2C). Phylogenetic signal was significant for only four traits (Table 5.2), being stronger for habits, breeding strategy and parental care. Hence, PD is not a surrogate for FD, as phylogeny is only related to trait diversity regarding 3 traits. Therefore, it is important to consider PD, as well as FD and trait diversity, because all these metrics account for some independent variability.

Variation in FD considering all functional components jointly, was best accounted for by mean forest patch and waterbody area in the 1500 m buffer ($F_{(8, 26)} = 35.84$, $p = 0.029$; Table 1); higher mean forest patch and waterbody area caused a 6.5 and 8.7% increase in functional diversity, respectively (Fig. 5.2A, B). Anuran biomass was mostly affected by distance to the closest waterbody, decreasing 95% with increased distance to the closest waterbody ($F_{(8, 26)} = 74.97$, $p = 0.021$; Fig. 5.2F).

Decomposing FD into its functional components revealed considerable heterogeneity regarding the effects landscape and local variables have on each trait's diversity (Table 5.1). Anuran activity diversity decreased 25% with increased distance to the closest waterbody ($F_{(9, 26)} = 79.44$, $p = 0.019$; Fig. 5.3A). Diversity in anuran habits was affected mainly by local waterbody characteristics, namely percentage of bare ground, increasing 47% with increased bare ground ($F_{(9, 26)} = 32.27$, $p = 0.031$; Fig. 5.3B). Diversity in anuran habitats was predicted by the number of waterbodies within the 500 m buffer, increasing 21% with higher waterbody abundance ($F_{(9, 26)} = 21.07$, $p = 0.033$; Fig. 5.3C). Diversity in adult snout-vent-length and anuran breeding strategy were mainly affected by local waterbody characteristics. SVL diversity increased 11% with increasing shrub height and percentage of shaded ground ($F_{(8, 26)} = 17.31$, $p = 0.044$; Fig. 5.3D, E). Breeding strategy diversity increased 56% with increased percentage of shaded ground ($F_{(9, 26)} = 19.20$, $p = 0.037$; Fig. 5.3F). Diversity in clutch size was mainly predicted by the distance to the closest waterbody, decreasing 25% with increasing distance to the nearest waterbody ($F_{(9, 26)} = 43.97$, $p = 0.021$; Fig. 5.4A). Diversity in parental care was mainly predicted by local waterbody characteristics, especially percentage of bare ground, and total waterbody area within the 1000 m buffer ($F_{(8, 26)} = 23.70$, $p = 0.031$; Table 5.1). Parental care diversity increased 33% with increasing percentage of bare ground, and decreased 23% with increasing total waterbody area within the 1000 m buffer (Fig. 5.4B, C). Range diversity was mainly affected by the total forest patch area within the 500 m buffer, increasing 24% with increased total forest area ($F_{(9, 26)} = 16.81$, $p = 0.046$; Fig. 5.4D).

The apparent departure from linearity in some relationships (Fig 5.2D, E; Fig. 5.2F; Fig. 5.4C) is caused by the insufficient sampling of waterbodies in the intermediate and maximum state regarding predictor variables. For example, regarding the relationships among TD and mean forest area, we apparently failed to sample more waterbodies within the intermediate and maximum amount of forest area within the 500m buffer. Hence, while the relation appears linear for those levels, there is a cluster of waterbodies with a small amount of forest area visually confounding the overall relationship.

The most significant predictors for the GLMM models were in agreement with the HP results, which determines the independent contribution from each predictor.

Table 5.1. Best fit model for each diversity metric, with estimates for the significant with largest independent contribution (hierarchical partitioning) and respective marginal and contitional R^2. MeanFoA1500 = Mean forest patch area (1500 m buffer); MeanWbA1500 = mean waterbody area (1500 m buffer); NrFo1500 = number of forest patches (1500 m buffer); MeanFoA500 = mean forest area (500 m buffer); DistCloserWb = distance to the closest waterbody; NrWb500= number of waterbodies (500 m buffer); TWbA1000 = total waterbody area (1000 m buffer); TFoA500 = total forest patch area (500 m buffer).

Dependent variable	Predictors	Estimates (SE)	Hierarchical partitioning (%)	Marginal R^2	Conditional R^2
FD	Intercept	0.958 (0.004)		0.444	0.751
	MeanFoA1500	0.018 (0.004)	24.82		
	MeanWbA1500	0.007 (0.005)	25.73		
PD	Intercept	-35.360 (4.164)		0.645	0.869
	NrFo1500	6.280 (2.634)	40.45		
TD	Intercept	0.376 (0.067)		0.400	0.743
	PCA4	0.047 (0.045)	18.78		
	MeanFoA500	-0.157 (0.084)	15.54		
Biomass	Intercept	128.05 (43.40)		0.505	0.867
	DistCloserWb	-58.79 (17.43)	64.71		
Activity	Intercept	0.851 (0.011)		0.370	0.621
	DistCloserWb	-0.045 (0.011)	83.605		
Habits	Intercept	0.808 (0.020)		0.452	0.764
	PCA1	-0.028 (0.011)	36.486		
Habitat	Intercept	0.919 (0.013)		0.578	0.797
	NrWb500	0.035 (0.007)	42.396		
SVL	Intercept	0.948 (0.005)		0.320	0.641
	PCA2	0.007 (0.003)	47.901		
B. Strategy	Intercept	0.774 (0.023)		0.737	0.904
	PCA1	-0.023 (0.008)	21.306		
Clutch size	Intercept	0.871 (0.011)		0.296	0.596
	DistCloserWb	-0.034 (0.009)	82.744		

Parental care	Intercept	0.810 (0.022)		0.699	0.888
	PCA1	-0.023 (0.010)	22.602		
	TWbA1000	-0.0831 (0.022)	17.633		
Range	Intercept	0.922 (0.030)		0.789	0.939
	TFoA500	-0.097 (0.024)	18.180		

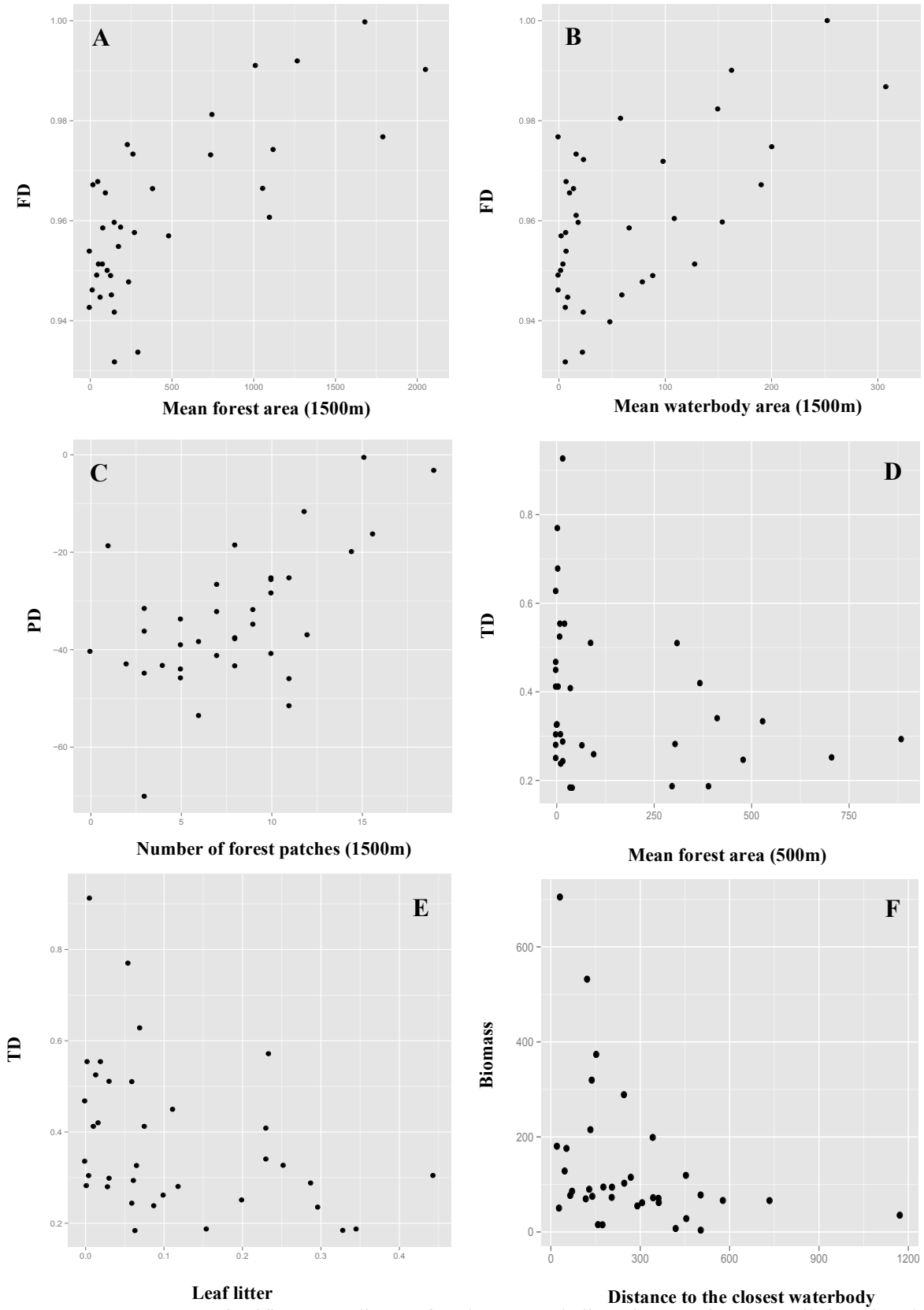

Figure 5.2. Most significant predictors for the general diversity metrics (overall functional diversity, phylogenetic diversitytaxonomic diversity) and total anuran biomass.

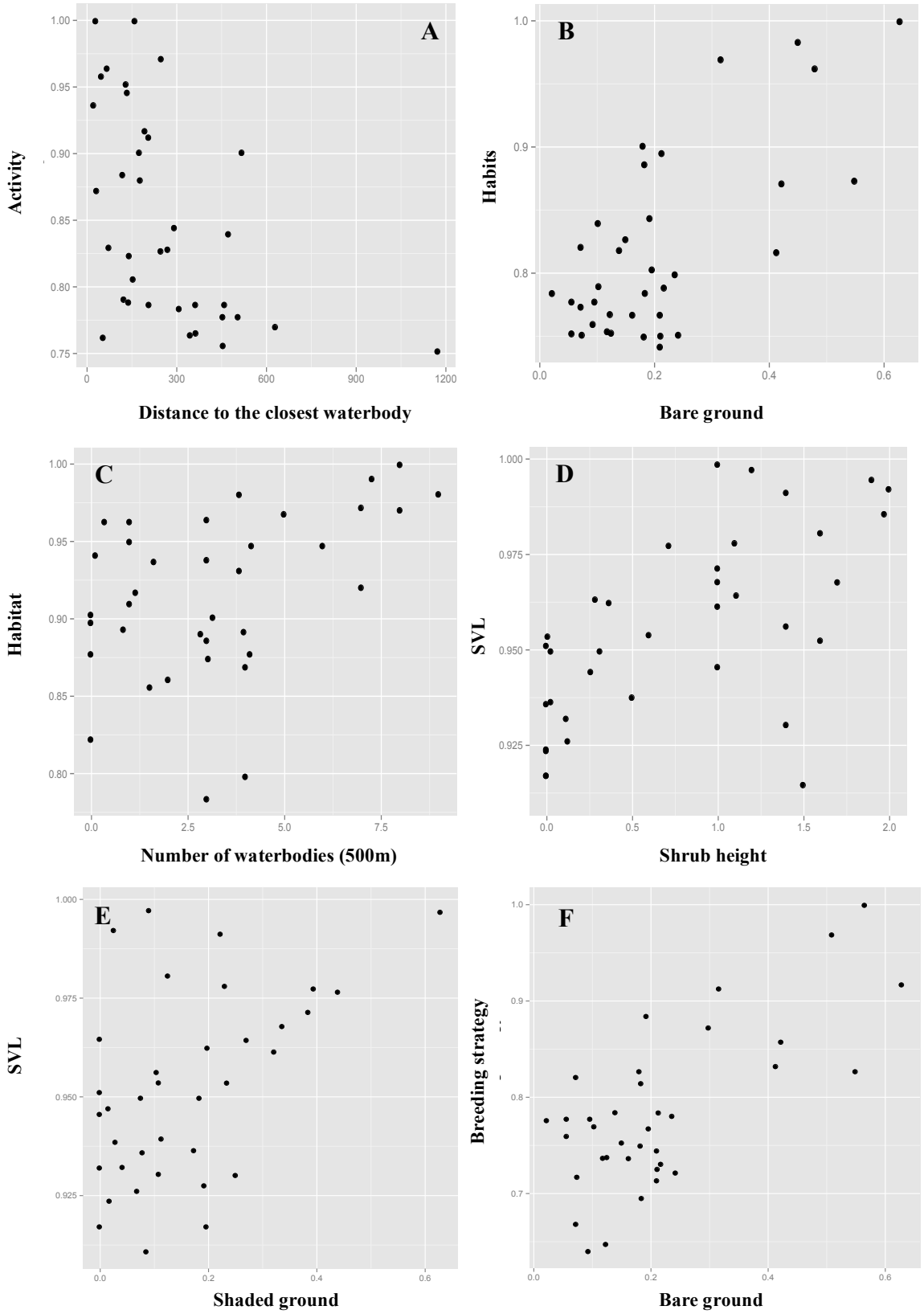

Figure 5.3. Most significant predictors for trait diversity (activity, habits, habitat, SVL and breeding strategy).

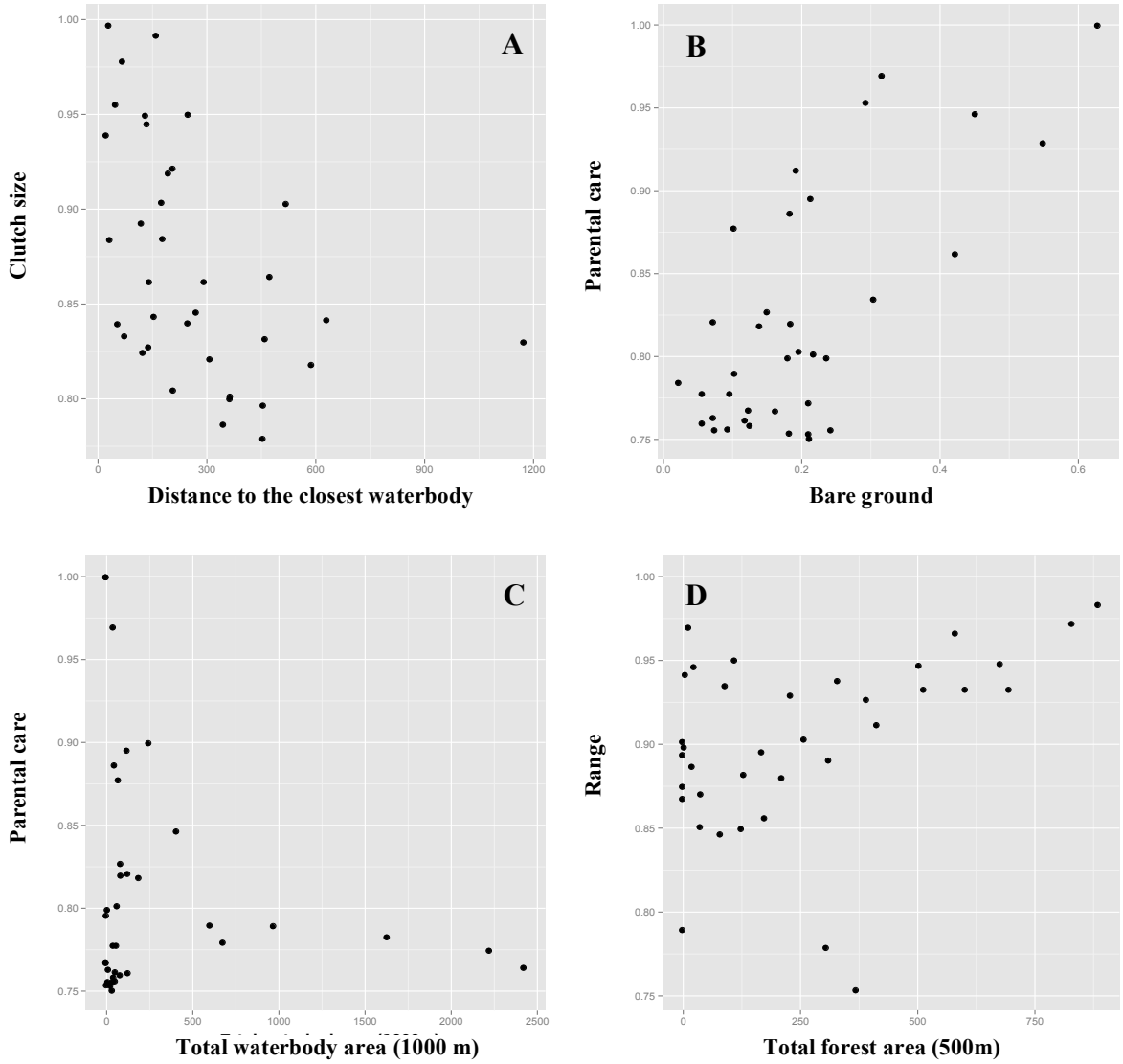

Figure 5.4. Most significant predictors for trait diversity (clutch size, parental care and range).

Table 5.2. Phylogenetic signal test for every trait used with respective significance value.

Trait	Obs.	Std. Obs.	P-value
Activity	-0.141	-0.877	0.920
Habits	0.722	4.346	0.001
Fossorial behaviors	0.343	2.772	0.037
Habitat	-0.196	-1.225	0.901
SVL	-0.125	-0.831	0.773
Breeding strategy	0.538	3.393	0.001
Clutch size	0.054	0.365	0.276
Parental care	0.671	4.006	0.005
Range	-0.059	-0.462	0.756

5.5. Discussion

Our study shows that communities from anthropogenic environments are shaped by multiple scale-dependent features. Furthermore, our trait-based approach allowed us to better understand how community assembly is shaped in human-modified landscapes, specifically how local and landscape features affect different facets of biodiversity.

Variation in TD was best explained by local waterbody characteristics and a compositional landscape variable, whereas variation in FD and PD were best explained only by landscape characteristics. This illustrates the complex ways in which human disturbances can affect different dimensions of biodiversity. Furthermore, it demonstrates how taking one diversity metric as the sole describer of biodiversity is too simplistic and may lead to erroneous conclusions and flawed management plans. Nonetheless, biodiversity is still seldom assessed using multidimensional and multi-scale approaches. To our knowledge, this was the first study to address the effects of local and landscape variables on multiple and complementary anuran diversity metrics in anthropogenic environments.

TD was lower in waterbodies with more terrestrial leaf-litter i.e., in waterbodies more marginal to rice crops, only partially embedded in rice crops. This, along with the association of lower TD with increased mean forest patch area within the 500 m buffer, may suggest that species prefer breeding inside forest patches (Becker et al. (2010)).

When forest patches are scarce, species tend to concentrate in waterbodies embedded in rice crops, causing increased species richness, due to low availability of better breeding sites.

Not all traits exhibited a phylogenetic signal, possibly indicating that PD represents differences in traits that were not considered for this study. Because community assembly processes act on traits, species' response to environmental variation may be reliably translated by the measured functional attributes (FD) or by unmeasured characteristics (addressed through PD). PD increased with increasing number of forest patches, which may be explained by the decreased PD in communities from rice crops compared to their pristine counterparts (Ribeiro et al. *in prep*). Waterbodies close to more forest patches exhibit higher PD because species living on those patches may be able to disperse and colonize waterbodies within rice crops if these are sufficiently close to ensure dispersal and survival. Similarly, variation in FD, which considers every functional trait jointly, increased with higher mean forest patch and waterbody area. Both dimensions highlight a pattern of increased diversity in waterbodies closer to many others and large forest patches, emphasizing the importance of forest patches and waterbodies in maintaining diverse anuran communities in agricultural landscapes. Distance from forest patch has been considered an important predictor of species richness, especially for species with low dispersal ability (Otto et al. 2007; Silva and Rossa-Feres 2011, Silva et al. 2011). Due to amphibian's ecophysiological limitations (Duellman and Trueb 1994), low mobility (Gibbs 1998), and high mortality during dispersal through roads or agricultural matrices (Becker et al. 2007), colonizing isolated ponds is impossible for some species and leads to selective exclusion from these waterbodies (Silva and Rossa-Feres 2011). PD and FD are important aspects of ecosystem resilience (Allen et al. 2005; Cisneros et al. 2014), the ability of ecosystems to absorb disturbances while maintaining key functions (Folke et al. 2004), increasingly crucial considering global changes and increased human pressure on ecosystems. Ecosystem resilience safeguards vital services upon which humans and biodiversity depend, such as seed dispersal, pollination, and pest control (Foley et al. 2005). Ecosystems are more resilient when every function is fulfilled by at least one species. Due to their ecological importance, loss of anuran diversity may

affect vital ecosystem processes and contribute to loss of system resilience and resistance (Davic and Welsh 2004).

The importance of landscape and local features for anuran assemblages was trait-specific. Anuran biomass and several traits (anuran activity, habitat, clutch size and range size diversity) showed increased diversity with increased waterbody proximity and area. Waterbody proximity, abundance and area has been determined as important for species diversity and abundance, often linked to the amphibian's need to avoid desiccation (Salazar et al. 2016). Due to diurnal environmental constraints, such as high temperatures and low humidity, most anurans from the Cerrado are nocturnal, while diurnal anuran are usually more associated to forest physiognomies (Olalla-Tárraga et al. 2009). Hence, distance to the closest waterbody may determine dispersion survival and, consequently, success in colonizing new waterbodies. Waterbody networks also offer increased shelter, calling, oviposition, and foraging site availability, in numerous waterbodies located relatively closer to each other. More isolated waterbodies may present increased desiccation risk during migration, as well as lower microhabitat availability, possibility with every shelter/oviposition/foraging site saturated, leading to competitive exclusion of some species (Becker et al. 2007, Russildi et al. 2016). Therefore, waterbody networks are especially important for amphibian communities in agricultural landscapes due to the often hostile conditions of those environments. Networks provide increased dispersion success, and higher availability of ecological niches, calling and oviposition sites, making them of the utmost importance for sustaining diverse anuran communities in agricultural landscapes.

Range diversity also increased with increasing forest area. The presence of forest patches in the vicinities of the waterbody allows the subsistence of less generalist species that probably use the patches as shelter and occasionally breed in agricultural waterbodies close by (Silva and Rossa-Feres 2011, Silva et al. 2011), causing an increased diversity in range size.

Anuran SVL, habits, breeding strategies and parental care diversity increased with increasing bare ground, vegetation height and shaded ground, expressing the ability that waterbodies more marginal to rice crops have to sustain increased trait diversity than

waterbodies embedded in the agricultural matrix. Indeed, both percentage of bare ground and vegetation height have been considered important for amphibian abundance and diversity, due to its direct influence on amphibian desiccation risk and reproductive success (Scheele et al. 2012, Cline and Hunter 2014). Larger anurans tend to incur in increased desiccation risk due a larger surface area, which may explain increased SVL diversity in marginal waterbodies, with increased shelter availability and microclimate stability, due to diverse marginal vegetation (Olalla-Tárraga et al. 2009). This explains why waterbodies embedded in rice crops appear to be mainly colonized by smaller species, with similar habits and breeding strategies. Marginal waterbodies offer increased microhabitat diversity and availability, hosting an increased diversity of species with diverse traits. Waterbodies embedded in rice crops offer little breeding site diversity, which explains why waterbodies marginal to the crops held increased diversity in traits related to breeding strategies.

Our study is the first to approach how scale-dependent features shape anuran functional and phylogenetic diversity in agricultural landscapes. Our results emphasize the importance of creating and/or conserving networks of abundant and large forest patches and waterbodies for sustaining higher levels of FD and PD in agricultural landscapes. As both PD and FD are known to greatly contribute to ecosystem resilience, we believe the patterns observed for anuran communities are of the utmost importance for managing of agricultural lands, especially in the tropics, where agricultural expansion is unrelenting and biodiversity is especially high and unique.

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“Look again at that dot. That's here. That's home. That's us. On it everyone you love, everyone you know, everyone you ever heard of, every human being who ever was, lived out their lives. The aggregate of our joy and suffering, thousands of confident religions, ideologies, and economic doctrines, every hunter and forager, every hero and coward, every creator and destroyer of civilization, every king and peasant, every young couple in love, every mother and father, hopeful child, inventor and explorer, every teacher of morals, every corrupt politician, every "superstar," every "supreme leader," every saint and sinner in the history of our species lived there-on a mote of dust suspended in a sunbeam.

[...]

Our posturings, our imagined self-importance, the delusion that we have some privileged position in the Universe, are challenged by this point of pale light. Our planet is a lonely speck in the great enveloping cosmic dark. In our obscurity, in all this vastness, there is no hint that help will come from elsewhere to save us from ourselves.

The Earth is the only world known so far to harbor life. There is nowhere else, at least in the near future, to which our species could migrate. Visit, yes. Settle, not yet. Like it or not, for the moment the Earth is where we make our stand.

It has been said that astronomy is a humbling and character-building experience. There is perhaps no better demonstration of the folly of human conceits than this distant image of our tiny world. To me, it underscores our responsibility to deal more kindly with one another, and to preserve and cherish the pale blue dot, the only home we've ever known.”

Carl Sagan, *Pale Blue Dot: A Vision of the Human Future in Space*

Chapter 6

Anuran functional connectivity in rice crops: a graph-theoretic approach.

6. ANURAN FUNCTIONAL CONNECTIVITY IN RICE CROPS: A GRAPH-THEORETIC APPROACH.

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6.1 Abstract

Habitat fragmentation is one of the major causes of biodiversity decline in agricultural landscapes. Enhancing connectivity among fragmented habitats is therefore pivotal for conservation planning. Amphibians are frequently characterized as having limited dispersal abilities, strong site fidelity and spatially distant breeding habitats. Hence, success in amphibian conservation, restoration or management can only be achieved by evaluating how structural connectivity relates to a species' functional connectivity. We performed graph-theoretic network analysis to a set of waterbodies embedded in rice crops, to estimate the importance of each waterbody to the connectivity of the entire network. We used anuran diversity metrics (taxonomic, functional and phylogenetic diversity) as proxies of anuran functional connectivity, as species diversity has previously been related with landscape connectivity. We found that forest patch area and abundance, as well as waterbody area in the vicinities of a waterbody, were the most important predictors of waterbody importance for connectivity. Although our approach of network analysis followed the simplest model, and cannot be generalized to other cases without caution, our results suggest that, in order to maximize pond network connectivity for amphibians in rice crops, we must ensure the existence of (i) abundant and large forest patches in the area surrounding waterbodies, and (ii) a network of abundant waterbodies.

Keywords: Meta-populations; dispersal; Neotropics; Cerrado; amphibians.

6.2 Introduction

Natural habitat loss and fragmentation are the main causes of biodiversity loss in agricultural landscapes (Liira et al., 2008). The effects of habitat fragmentation on species richness and composition have been extensively studied (Ockinger et al., 2010). However, little is known about how fragmentation affects other facets of biodiversity, such as functional or phylogenetic diversity. Fragmentation can indeed affect plant functional diversity directly (e.g. by promoting traits associated to long distance dispersal when fragment isolation increases) and indirectly (e.g. by decreasing species richness, hence trait diversity, when fragment area decreases) (Magnago et al., 2014; Sonnier et al., 2014). Certain ecological traits, such as naturally low population size, strong habitat specialization, large body size and low mobility have been shown to be associated to a increased sensitivity to fragmentation in some vertebrate groups (Ewers and Didham, 2006; Henle et al., 2004; Laurance, 1991; Viveiros De Castro and Fernandez, 2004). A common explanation for this phenomenon is that habitat fragmentation may filter species with particular sets of traits, leading to trait convergence (Grime, 2006) and decreased functional diversity. Although the identification of these traits is critical for designing species-specific conservation strategies (Kotiaho et al., 2005; Purvis et al., 2000), few studies have addressed the effects of habitat fragmentation on functional or phylogenetic diversity.

A wide range of measures has been developed to quantify habitat connectivity that either measure structural or functional connectivity (Tischendorf and Fahrig, 2000). Structural connectivity can be easily determined, for example, by calculating landscape metrics obtained from geographic information systems, or simply by estimating geographic distances among habitats or populations. Because it is easily measured, structural connectivity is often used as a proxy for functional connectivity, although the response of species may not necessarily be equivalent to the spatial configuration and composition of a landscape (Tischendorf and Fahrig, 2000). Functional connectivity can be measured either by directly observing the movement of species, for example, by radio-tracking or mark-recapture studies, or indirectly by using population genetic data (Keller et al., 2010).

Enhancing connectivity among fragmented habitats is a major goals of conservation

planning (Brückmann et al., 2010). However, success in conservation, restoration or ecological management can only be achieved by evaluating to which degree an increase in structural connectivity (for example, the creation of stepping stones) improves the functional connectivity of target species. Because structural connectivity is generally used as an equivalent of functional connectivity in conservation, ecological literature and even management plans, it may lead to inaccurate and unsuccessful conservation schemes (Taylor et al., 2006).

Models such as "least cost path analysis" (e.g., LaRue and Nielsen, 2008), or "graph-theoretic" models are often used to study connectivity and aid in management planning. One of the most popular approaches in meta-population ecology, is patch-based monitoring, wherein species occupancy is recorded in a network of discrete habitat patches of varying size and isolation. Attributes of the habitat patches, matrix areas, and/or the species of interest are used in a modeling framework to determine how strongly connectivity and other factors influence species occupancy, colonization, or extinction probabilities. Patch connectivity can be measured in a variety of ways, from the simplest nearest-neighbor distance to more complex formulas that include patch distances, areas, species dispersal abilities, and other scaling parameters (Hanski 1994b).

Graph-theoretic connectivity metrics combine the attributes of habitats and populations with the dispersal behavior of species (Saura and Pascual-Hortal, 2007). In graph-theoretic approaches, the habitat patches or populations (nodes) are connected by links, for example, geographic distances (Saura and Pascual-Hortal, 2007; Saura and Torné, 2009). Nodes are considered connected if the internode distance is lower than, for example, the maximum dispersal distance of a focal species (that is, structural connectivity). Based on the topology of a network, it is possible to determine the most critical network elements—nodes as well as links—for maintaining the structural connectivity of habitat patches or populations in a landscape. Graph theory (Harary, 1977) has been taken from its original mathematical context and is nowadays applied to many other purposes, such as understanding biological process as food webs, community stability and gene networks (Proulx et al., 2005). This approach has been

suggested as a useful tool in assisting decision making for conservation purposes (Saura and Pascual- Hortal, 2007). The application to landscape ecology is not new (Risser et al. 1984) but it was not until recently that it started to be used for conservation practices (Jordán et al., 2007; Minor and Urban, 2008; Vasas et al., 2009). Despite the increasing application of graph-based connectivity metrics in recent years, studies relating these measures to estimates of functional connectivity, such as gene flow, or to genetic diversity, remain scarce (Dyer et al., 2012; Neel, 2008).

Amphibians are the most endangered vertebrates worldwide (Wake and Vredenburg, 2008). Due to their biphasic life cycle, highly permeable skin and ectothermic physiology, amphibians are very dependent on environmental quality and vulnerable to its change (Niemi and McDonald, 2004). These specificities, combined with their restricted dispersal ability (Bowne and Bowers, 2004; Russell et al., 2005), demand an integrated local and landscape-level approach when planning for amphibian conservation and habitat management. Pond breeding amphibians have reproductive populations associated with ponds distributed over the landscape, being often considered to follow meta-population dynamics (but see Smith and Green, 2005). Thus, landscape connectivity and, specifically, pond connectivity is of extreme importance for the long- term persistence of these populations, since it may buffer the stochastic events to which ponds (particularly Mediterranean ponds) are extremely prone (Compton et al., 2007; Cushman, 2005) Amphibians play keystone roles in ecosystem functioning, act as both predators and prey, enable nutrient transport between aquatic and terrestrial systems and are among the most diverse and abundant vertebrates, comprising species from a variety of habits, breeding strategies and dispersal abilities. Hence, the importance of amphibian communities is intrinsically related to vital ecosystem processes and, consequently, ecosystem resilience and resistance (Davic and Welsh, 2004).

In this study, we applied network analysis to a set of waterbodies whose amphibian communities were sampled, in order to establish the structural importance of each individual waterbody to the connectivity of the entire network. With this procedure, we characterize each waterbody regarding relative connectivity and corresponding amphibian diversity. The latter has previously been related with landscape connectivity (Bailey et al., 2010) and, although, with

constraints, it is a very straightforward measure of biological response to the environment. Since connectivity is not the only parameter that influences suitability of a waterbody for amphibians, we added several local waterbody (e.g., percentage of bare ground, herbaceous vegetation, shrubs and trees, aquatic vegetation) and landscape characteristics (e.g. distance to the closest waterbody, total waterbody area and total forest patch area within a 500 m buffer) considered important for amphibians. We intend to assess the relation between each waterbody importance for connectivity with those variables, in order to better contribute to more effective management recommendations. First, we evaluated whether graph-based estimates of structural connectivity reflect functional connectivity, measured as anuran taxonomic, functional and phylogenetic diversity. Afterwards, we examined the relationship between local and landscape pond characteristics on waterbody importance for connectivity. We hypothesized that forest patch area and waterbody structural heterogeneity would affect pond importance for connectivity in the agricultural matrix.

6.3 Methods

6.3.1 Study area and sampling design

This study took place in an ecotone region between the Amazon rainforest and the Brazilian savanna, the Cerrado, in the state of Tocantins, Brazil. Sampled rice crops are located in the municipal district of Lagoa da Confusão. The agricultural landscapes of the Cerrado-Amazon ecotone are characterized by the presence of ipucas, "islands" of closed native vegetation which remain flooded longer than the surrounding areas. These structures are characterized by the abundance of certain plants (e.g. *Calophyllum brasiliense*) and presence of endemic animals (e.g. *Rhipidomys ipukensis*). Because converting an ipuca into cropland results in very low crop yields, due to their inherent inappropriateness for agricultural exploration, the agricultural landscapes of the Tocantins state are quite peculiar, with vast crop areas speckled

by many “islands” of native vegetation of variable dimensions.

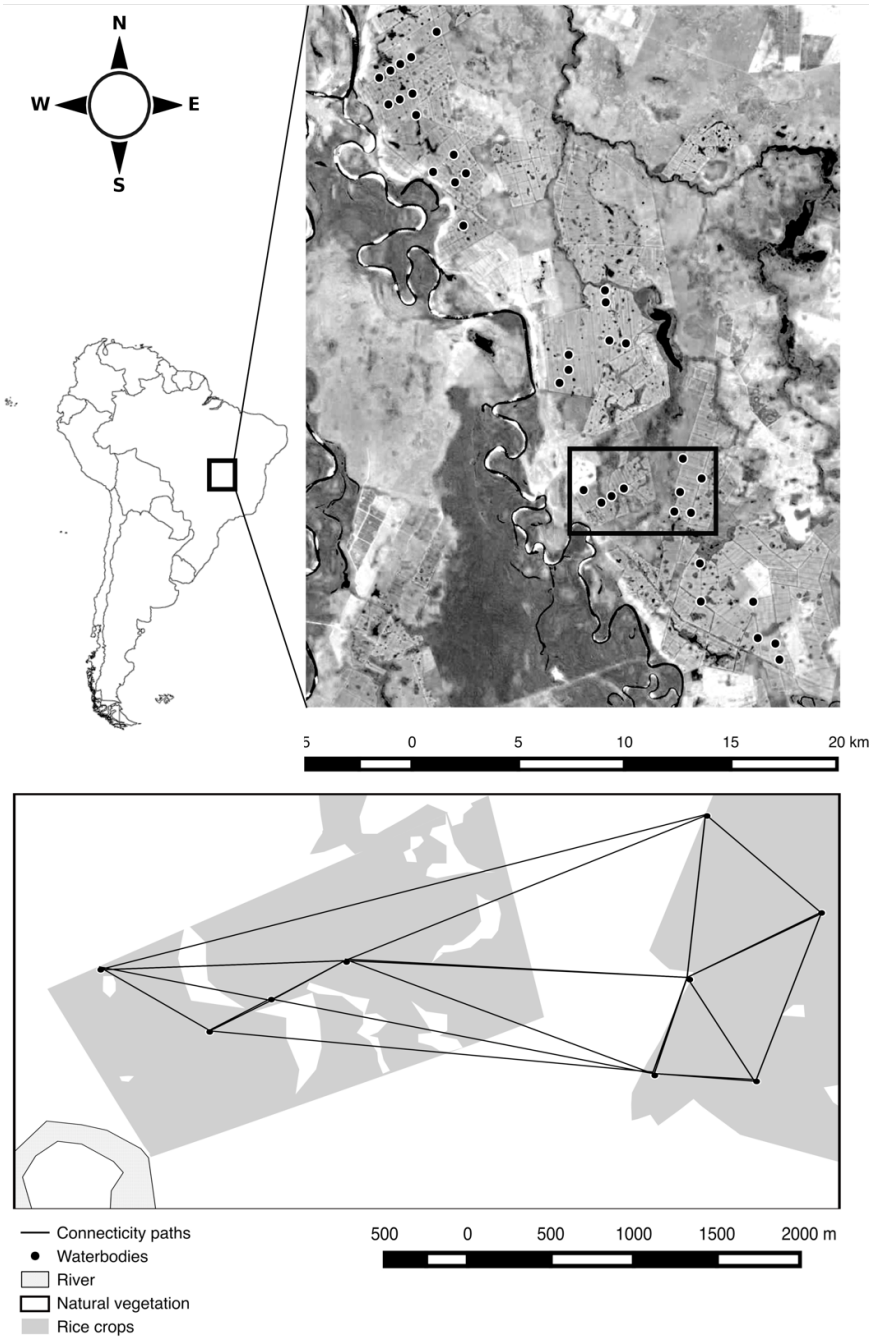

Figure 6.1. Study area and design with paths possibly taken by dispersing anurans between a set of waterbodies. Dark circles represent the waterbodies sampled.

The region is a seasonally flooded area, with two large rivers, Formoso and Javaés, and a very pronounced rainy season from October to April.

Irrigated rice fields in the Cerrado-Amazon ecotone present a dynamic hydrologic regime, with variation between aquatic and terrestrial phases. When rice is being grown, from December to April, rice fields remain with surface water until harvest, before which crops are completely drained. After rice harvesting, crops may remain fallow or other crops, such as soy or watermelon, may be cultivated, depending on the landowner's will. Besides rice fields, the region's landscape is also occupied by pasture areas, where cows, emus or water buffalos roam.

In order to ensure that we represented most of the environmental variability of this agricultural landscape, a total of 10 rice fields were chosen along the Rio Formoso irrigation project (Fig. 6.1). Rice fields varied in size, *ipuca* abundance and dimensions and waterbody abundance and size. We selected 3 to 4 lentic waterbodies for anuran sampling in each rice field, totalizing 35 waterbodies. Waterbodies were chosen based on type, size and hydroperiod. We chose small (25 m^2) to large (1200 m^2) temporary lentic waterbodies.

6.3.2 Anuran surveys

Agricultural surveys were conducted during two rainy seasons, from February 2013 to April 2014. Anuran sampling was performed using nocturnal visual encounter surveys along the 10 m wide margin of each waterbody, for approximately 30 min. Every individual seen perched on the vegetation, on the floor, under the leaf litter, logs or stones was caught, identified, measured, weighed, photographed and then released near the site of origin.

6.3.3 Local waterbodies characteristics

Environmental variables such as percentage of bare ground, herbaceous vegetation, shrubs, trees, shaded ground, leaf litter, logs/rocks, aquatic vegetation, herbaceous vegetation height,

shrub vegetation height, herbaceous vegetation heterogeneity and shrub vegetation heterogeneity were registered. These variables were quantified performing transects (10 m long x 1 m wide) set on the sampled waterbody margin. For every meter, a 50 cm x 50 cm grid would be placed above the ground and the number of squares with 50% or more coverage of each variable would be summed and divided by the total (25 squares).

6.3.4 Landscape features

We quantified landscape structure for each waterbody using Google Earth satellite imagery representing the landscape of the year 2014 and corroborated the main features on the field. For each of the 35 sampled waterbodies, we quantified distance to the closest waterbody, distance to the closest forest patch and number of waterbodies, number of forest patches, total waterbody area, total forest area, mean forest patch area and mean waterbody area within 500 m, 1000 m and 1500 m buffers. While compositional features, such as number of forest patches or total waterbody area describe the proportions of different types of land use within the area surrounding a waterbody, configurational features, such as distance to the closest forest patch or waterbody, specify the geometric arrangement of land features surrounding a waterbody. We quantified landscape characteristics at three spatial scales (buffers of 500, 1000 and 1500 m radius) that we found significant for amphibians, regarding known dispersal abilities, to account for interspecific differences in anuran dispersal and ability to endure in agricultural systems.

6.3.5 *Trait Data*

We compiled life history and ecological traits for every anuran species registered in the agricultural and pristine study areas. For each species we compiled information of 12 traits: activity, habits, habitat, fossorial behavior, adult snout-vent length (SVL), breeding site, breeding strategy, clutch size, parental care, breeding season, breeding pattern and geographic range size. We chose these traits based on perceived importance for determining species resilience to agricultural activities (Table A1) and on data availability. We compiled trait data from the literature, the AmphibiaWeb and IUCN online databases. If published data were unavailable, we relied on expert opinion or inferred trait information based on closely related

species. Because breeding site, breeding season and breeding pattern were very homogeneous along the agricultural anuran community, we decided to exclude these three traits from the following analyses.

6.3.6 Biodiversity metrics

We quantified TD at each site, using Simpson's diversity index (Simpson, 1949), and FD and PD using Rao's quadratic entropy (Botta-Dukát, 2005). These metrics facilitate comparison among these three dimensions because Rao's Q is an extended form of Simpson's index that includes information on species dissimilarities. Rao's Q corresponds to the sum of functional or phylogenetic distances between all species, weighted by the product of their relative abundances and describes the abundance- weighted average difference among species from a community (Weiher, 2011). Functional and phylogenetic distances between species were obtained from pairwise dissimilarity matrices for all traits combined and for the phylogeny. Functional pairwise dissimilarity matrices were calculated using the Gower distance matrix, which quantifies dissimilarities with categorical and numeric attributes simultaneously (Botta-Dukát, 2005). To promote meaningful comparisons among dimensions, we transformed each metric into its effective number of species (Jost, 2007), allowing direct interpretation of differences among indices (Jost, 2007). We calculated FD with function dfFD from package FD, and PD and TD with function raoD from package picante on program R.

6.3.7 Network analysis

Studies on dispersal ability of amphibians reveal that the maximum walked distance is very variable among species (Kovar et al., 2009; Smith and Green, 2005), ranging from 10 to 2000 m. We therefore, established four thresholds: 250, 500, 800 and 1000 m. We then tested at which threshold the relationship with anuran diversity lost significance. For each threshold and diversity metric, we calculated node importance for connectivity of the entire pond network. We used correlation analysis to relate the waterbody importance for connectivity to the diversity

metrics of the pond-breeding amphibians.

Nodes were characterized by three diversity metrics (TD, FD and PD), and links were represented using Euclidean distances between meta-populations. Species richness has previously been related with landscape connectivity (Bailey et al., 2010) and used to assess pond network connectivity for amphibians (Ribeiro et al., 2011). Although with constraints, it is a very reliable measure of biological response to the environment. We used taxonomic diversity, but also functional and phylogenetic diversity to assess pond connectivity, as both FD and PD constitute more accurate representations of anuran diversity, dispersal constraints and more thorough guidance for management actions.

Two graph-based connectivity indices, the integral index of connectivity (IIC) and the probability of connectivity (PC), have been shown to perform best for the purpose of prioritization of habitats and links (Saura and Pascual-Hortal, 2007; Saura and Torné, 2009). We chose IIC for evaluating the importance of each waterbody for connectivity. IIC ranges between 0 and 1 and is defined as:

$$IIC = \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{a_i a_j}{1 + nl_{ij}}$$

where n is the total number of nodes in the landscape, a_i and a_j are the attributes of nodes i and j and nl_{ij} is the number of links (distances) between nodes i and j. IIC is based on a binary connection model that means that two nodes are either considered connected or not depending on the actual distance between them in relation to the predefined distance threshold. In CONEFOR 2.6, the prioritization of each node for maintaining landscape connectivity is calculated as the percentage of the variation of IIC resulting from the removal of a given node from the landscape:

$$dl(\%) = 100 \times \frac{I - I_{remove}}{I}$$

where I is the overall index value (IIC) for all initially existing nodes in the landscape, and I_{remove} is the overall index value after the removal of a given node from the landscape. To estimate the effects of landscape variables on taxonomic, functional and phylogenetic diversity as a measure of functional connectivity, we used Euclidian distance, and the local and landscape variables for each waterbody.

6.3.8 Quantitative analyses

We performed generalized linear mixed models (GLMMs) to examine the effects of local and landscape features on waterbody connectivity considering TD, FD and PD as anuran diversity metrics.

Because the 1000 and 1500 m buffers used to characterize the surroundings of each waterbody included other waterbodies within the same rice field, we used rice field as random effect. Random effects are especially useful for inferring on a population when the data available are random samples of that population, assuming it is a meta-population, and that our sample reflects many draws from that population. So rather than anchoring results around heterogeneous intercepts, the data will be used to elucidate the parameters of that distribution from which data were drawn.

Model fit for each dependent variable was manually assessed from the null model, to avoid automatic variable elimination for the sake of model fit optimization only. We choose to assess model fit and predictor significance through F-tests performed among nested models for connectivity described by FD, PD and TD. We progressively evaluated each predictor's significance, and then fitted reduced models with the most significant predictors, finally assessing the reduced models' fit against the full model, using F tests. We fit all models using the lme4 package (Bates 2007).

We performed hierarchical partitioning (HP) to further determine the relative independent importance of each significant variable. We determined the statistical significance

of each independent variable's independent contribution using a randomization approach with 5000 iterations and an alpha- level of 0.05 (Mac Nally, 2002). We executed hierarchical partitioning using package 'hier.part' (MacNally & Walsh, 2004).

6.4 Results

The effects of structural graph-theoretic connectivity measures on taxonomic, functional and phylogenetic diversity were different but consistent. Depending on the distance threshold considered, we detected significant correlations between node importance and estimates of diversity. TD was significantly correlated to node importance considering the 250, 500 and 800 m thresholds (r_{250}=0.81, p-value = 3.721e- 09; r_{500}=0.81, p-value=3.721e-09; r_{800}=0.64, p-value=3.291e-05). FD was significantly correlated to node importance in the 250 and 500 m thresholds (r_{250}=0.51, p-value = 0.001705; r_{500}=0.51, p-value = 0.001705). PD was significantly correlated to node importance considering three thresholds (r_{250}=0.66, p-value = 1.812e-05; r_{500}=0.66, p- value = 1.812e-05; r_{800}=0.55, p-value = 0.000608).

Local variables were important predictors of node importance regarding taxonomic, functional and phylogenetic diversity (Table 6.1). Regarding TD and PD, node importance decreased with increasing shaded ground. Regarding FD, node importance increased with increasing abundance of shrubs and trees in the waterbody margin.

The most important landscape predictors of node importance were also consistent. Number of forest patches, total forest area and mean waterbody area in the vicinities of the waterbodies were the most important predictors of node importance for connectivity regarding the three diversity metrics used (Table 6.1). Regarding TD, waterbody importance increased 7% with total forest area and number of forest patches (Fig. 6.2A, B). Regarding FD, node importance increased 83% with increasing mean waterbody area in the vicinities of the waterbodies (Fig. 6.2C). Regarding PD, node importance increased 8% with increasing number of forest patches and total forest area in the vicinity of each waterbody (Fig. 6.2D, E).

The most significant predictors for the GLMM models were in agreement with the HP results (Table 6.1), which determines the independent contribution from each predictor.

Table 6.1. Independent contributions of significant predictors of node importance considering TD, FD and PD as diversity metrics and two distance thresholds (250 and 800m).

Diversity metric$_{threashold}$	Local predictors	Hierarchical partitioning (%)	Landscape predictors	Hierarchical partitioning (%)
TD_{250}	-	-	Total forest area (1000m)	52.16
			Mean waterbody area (500m)	13.14
			Number of waterbodies (500m)	12.27
TD_{800}	Shaded ground	22.65	Number of forest patches (1000m)	32.40
	Leaf-litter	19.38	Number of waterbodies (1000m)	26.22
	Bareground	17.87	Mean waterbody area (500m)	13.34
FD_{250}	Shrubs & Trees	44.50	Mean waterbody area (500m)	26.77
	Leaf-litter	31.40	Total forest area (1000m)	13.49
	Herb. vegetation	12.87	Total forest area (1500m)	9.60
PD_{250}	-	-	Total forest area (1000m)	38.60
			Mean waterbody area (500m)	20.45
			Distance to the closest waterbody	9.78
PD_{800}	Shaded ground	19.56	Number of forest patches (1000m)	30.56
	Leaf-litter	20.01	Number of waterbodies (1000m)	22.79
	Bareground	21.96		11.45

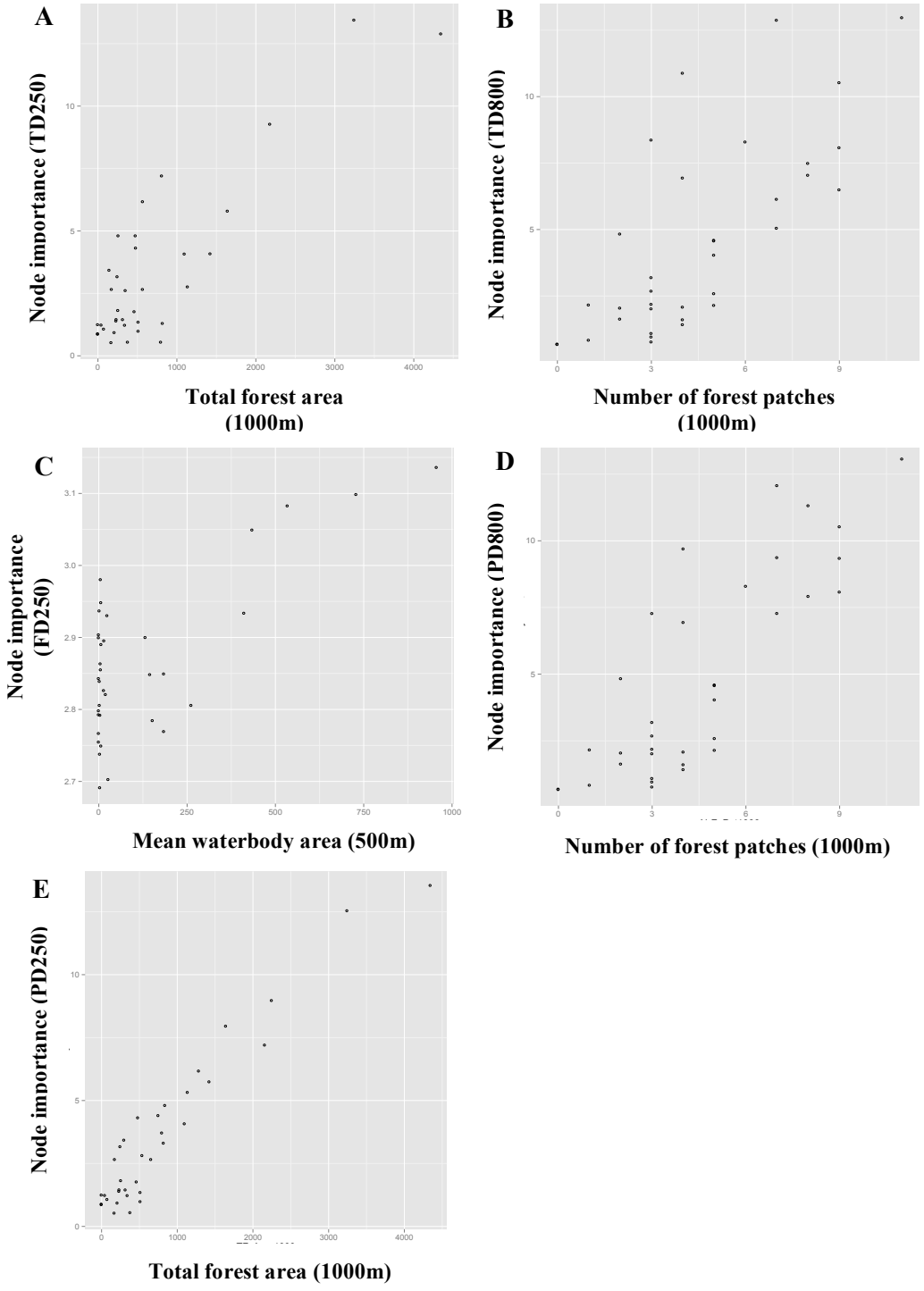

Figure 6.2. Most significant predictors of waterbody importance for connectivity using TD, FD and PD as proxies for functional connectivity.

6.5 Discussion

The significant positive relationship between anuran diversity metrics and pond importance clearly demonstrates that there is an association between structural and functional connectivity. The adoption of TD, FD and PD as proxies for functional connectivity is based on the premise that more accessible sites will host more species, traits and lineages, considering habitat suitability is equal. Regarding TD, the most accessible waterbody will host more species. Regarding FD, more traits will be represented in a waterbody widely accessible to the trait ensemble of the local community. Regarding PD, more lineages will be represented in the most accessible waterbodies.

Node importance depends on amphibian functional connectivity, in this case represented by anuran diversity metrics. Given that diversity metrics also represent habitat suitability, as more species will breed successfully in more suitable waterbodies, functional connectivity may be overestimated if those factors related to habitat quality are not accounted for. Hence, we regressed node importance measured according to the three proxies of functional connectivity against local habitat and landscape variables. Functional connectivity can only be affected by species intrinsic dispersal ability or by landscape features.

Amphibian functional connectivity within this agricultural landscape was positively related to node importance at distance thresholds between 250 and 800 m, depending on the metric used. The relation of the landscape connectivity with anuran diversity metrics is unambiguous, indicating that the accumulation of amphibian species, traits and lineages in breeding ponds is, even if partially, related to the spatial position of the pond in relation to the other ponds nearby. Our results corroborate those found by Cunningham et al. (2007) and Ribeiro et al. (2011). In fact, according to Cunningham et al. (2007), wetland connectivity is the best variable in distinguishing wetlands with high amphibian species richness from those with low species richness. Although species richness is an elementary measurement of regional diversity and extremely useful in conservation planning, it could be misleading and simplistic, as accounting only for species number leaves important community and ecosystem-level

parameters unassessed. For example, in this study the maximum distance threshold at which structural and functional connectivity were correlated was 500 m regarding trait diversity (FD) and 800 m regarding taxonomic and phylogenic diversity. This means that if traits related to low dispersal ability were represented by only one or two species that are unable to disperse beyond 500 m, they would not be represented in waterbodies beyond that threshold. However, this absence would probably not be translated into significantly lower taxonomic or phylogenetic diversity, which illustrates the importance of taking more that a single avenue to reach conclusions on the effects on anthropization of biodiversity.

Pond breeding amphibians typically exist in local populations associated with discrete breeding pools. With low dispersal ability and the potential for asynchronous dynamics among local populations, meta-population dynamics may play an important role in long-term population persistence (Gamble et al., 2007; Semlitsch, 2002; Smith and Green, 2005), especially in unstable anthropogenic landscapes. Hence, conservation efforts limited to the protection of individual pools may be ineffective over the long term if connectivity among pools is not maintained (Gibbs and Shriver, 2005; Gibbs, 1993). Indeed, maintaining and enhancing spatial connectivity among fragmented natural and semi-natural habitats is one of the main challenges for ecological management and conservation biology. However, although the structural properties of landscapes are widely used as indicators of biodiversity in practical landscape planning, they may not have a straightforward effect on functional connectivity, i.e., the way each species responds to landscape structure (Tischendorf and Fahrig, 2000). In this study, we used several local and landscape variables and a graph-theory based index to assess which features are more determinant for increasing waterbody importance for connectivity in a pond network embedded in an agricultural landscape. We found that total forest patch area and abundance within 1000 m from a waterbody, and mean waterbody area within the 500 m from a waterbody, were the most important predictors of node importance for connectivity.

The importance of forest fragments for dispersal in anthropogenic landscapes has been identified before. Janin et al. (2009) found that the landscape matrix strongly influenced toad occurrence, with forests and meadows causing low resistance to toad movement, and crops posing intermediate to high resistance to toad movement. Popescu and Hunter (2011) found

clear-cuts to be significant barriers to amphibian dispersal, altering the movements of emigrating juveniles from waterbodies. The low permeability of clear-cuts and other open-canopy habitats to juvenile amphibian movement has been previously recorded (Rothermel and Semlitsch, 2002; Rothermel, 2004). Hence, promoting the persistence of amphibian populations in anthropogenic landscapes must involve the preservation or creation of forest habitats adjacent to breeding sites (Todd et al., 2009).

Although our approach of network analysis followed the simplest model (euclidean distance and no weighing of the different ponds), and cannot be generalized to other cases without caution, our results suggest that in order to maximize pond network connectivity for amphibians in rice crops we must ensure that abundant and large forest patches are present in the vicinities of the waterbodies, and that we must create or preserve a network of abundant waterbodies.

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“Unless someone like you cares a whole awful lot,

Nothing is going to get better. It's not.”

Dr. Seuss, *Lorax*

Chapter 7

General discussion and Conclusions

7.1. Effects of anthropization on the Cerrado anurans

The Cerrado is currently under major anthropogenic pressure and the limited knowledge available on the biome's biodiversity is evident; new species are constantly being described and large portions of the biome have never been adequately sampled. Unfortunately this poses a very clear impairment on the development of effective management and conservation plans.

The anurofauna of the Cerrado has a series of ecophysiological traits that may render them more resistant to anthropic disturbances than Neotropical forest anurans. Characteristic fossorial habits and specialized breeding structures such as foam nests might in fact be responsible for the increased resistance of some Cerrado anurans in disturbed habitats, such as crops and pastures. However, much like what has been acknowledged in other biomes, anthropogenic areas are dominated by widespread, generalist species. Hence, although crops and pastures can harbor a seemingly diverse anuran community, there will be a strong dominance by resilient species, favoring generalists and excluding anuran specialists. Nonetheless, natural vegetation fragments, earthen irrigation channels and shallow depressions that support perennial ponds and aquatic vegetation appear to be important landscape features for promoting the use of rice fields by anurans.

The massive and omnipresent use of agrochemicals in the Cerrado is bound to act synergistically with crop and pasture setting and management. In fact, the scarce studies available identified pesticides on living tissue of generalist species, which may indicate that even these seemingly resilient species have low fitness. Furthermore, chytridiomycosis has also been recorded in many species extant in the biome, including Cerrado endemics. Given the declines this disease is known to cause, it may be causing severe unacknowledged declines.

The Cerrado anurofauna appears to be especially sensitive to the development of hydroelectric projects, as even previously common, widespread and generalist species declined or disappeared after flooding.

Latest predictions indicate that the occupation of the Cerrado will proceed northwards, dramatically reducing the proportion of remaining natural habitats, in synergy with climate change, leading to a great loss of biodiversity. Only a small portion of suitable

natural habitats will remain in northern Cerrado, with amphibian richness being reduced to less than half. Future climate changes will be especially detrimental for endemic anurans, with small potential current distribution.

This review allowed me to conclude that, contrary to widespread belief, the biodiversity of the Amazon is not the only one enduring aggressive threats in Brazil. The anurofauna of the Cerrado is under an unacknowledged high extinction risk and in urgent need of more scientific studies and conservation and management projects. It is urgent to direct the attention to the Brazilian savanna. The scientific community must help establish the Cerrado as a valuable biome with major ecological importance. Detailed demographic and community-level studies on Cerrado amphibians are badly needed, namely abundance and diversity studies for adult, juveniles and larvae/eggs.

7.2. Conservation priorities for the anurofauna of the Cerrado

In spite of the broad and aggressive character of the anthropogenic conversion of the Brazilian Cerrado, species do not respond equally to the same threats. The most vulnerable anurans in the Cerrado are a highly non-random subset of the anurofauna, composed of lotic breeders and habitat specialists with small clutches, large body sizes and small geographic ranges. Specialization has been associated to increased susceptibility to environmental change. Variables describing direct human impacts apparently had no effect on extinction risk, perhaps because populations of threatened species may have already been extirpated from the most disturbed habitats before assessments occurred (Cardillo et al., 2005; Tingley et al., 2013) or detrimental effects of anthropogenic activities have such broad, across species consequences, that end up being detrimental to all species.

This particular study demonstrates that the extinction risk of amphibians worldwide may be severely underestimated, especially in scarcely studied and highly anthropic biomes. A large proportion of species predicted as sensitive and/or decreasing is currently listed as LC or DD by the IUCN Red List. Given the difficulties intrinsic to studying amphibians, adopting predictive integrative trait-based approaches may give us insight into “accidents waiting to happen” and help prioritize regions for scientific projects or conservation actions.

The center of the Cerrado is the biome's main hotspot for high extinction-risk anurans and about 70% of the anuran species considered are major conservation gaps, while only 29 species are adequately protected. Hence, not only the extinction risk of the Cerrado anurofauna appears severely underestimated, but also the current PA network is insufficient to protect at least 50% of the minimum area required for ensuring the protection of 141 species.

This study underscores the importance of adopting more specific and integrative approaches to extinction risk, considering species ecology and landscape metrics to better guide conservation and management policies. The cost-effective and integrative approach we presented may be of special value for biodiverse regions, with strong anthropogenic pressure, but weak government support and scarce funding for conservation actions. Brazil is currently experiencing extremely high economic demands and, after long decades of raising public awareness to the importance of protecting the Amazon rainforest, other biomes have been targeted to fulfill social and economic pressures. Frameworks such as ours may shed light into which areas and species need more protection and what is the minimum protection each species needs to endure.

7.3. Neotropical anuran communities from rice crops

Habitat conversion and agricultural management caused profound alterations to the anuran community of a Cerrado-Amazon ecotone area, with dramatic loss of species diversity and functional richness and increase in functional divergence. Community composition suffered severe alterations, resulting in dominance of generalist hylids and leptodactylids and low representation of specialist microhylids and bufonids. Anuran communities in rice fields exhibited decreased phylogenetic diversity and mean phylogenetic distance, and increased mean nearest phylogenetic distance, suggesting that anuran communities in agricultural areas are composed of a few phylogenetically related species and, therefore, not as diverse as their pristine counterparts.

Functional and phylogenetic diversity indices provide deeper insights into the complex effects that disturbances have on biodiversity (Cornwell et al., 2006). Functional richness in particular has been invoked as a good predictor of ecosystem services because it describes species traits and represents the capacity of each species to provide a particular service (Díaz

and Cabido, 2001). Our study corroborates such conceptions because, although anuran species richness, functional richness and phylogenetic diversity were significantly lower in rice fields, taxonomic diversity did not vary significantly. Amphibians play keystone roles in ecosystem functioning; in food webs, they act as both predators on invertebrates and small vertebrates and as prey for larger animals, establishing an avenue for nutrient transport between aquatic and terrestrial systems. Loss of amphibian functional richness and increased functional divergence may affect vital ecosystem processes and contribute to loss of system resilience and resistance (Davic and Welsh, 2004).

Understanding how species traits correlate with their responses to agriculture will allow better predictions of the functional effects of anthropogenic land-use (Newbold et al., 2013). Diversity itself is an important component of ecosystem resilience because diverse communities are more likely to hold multiple species capable of contributing to a single given function. Small geographic ranges, association with forest and open area habitats, small clutches and large body size were associated with low to null species abundances in rice fields. However, our results show that the conversion of natural Cerrado-Amazon vegetation to vast rice fields results in such environmental stresses, that large subsets of species are driven to local extinction irrespective of their specialization. Species commonly perceived as resilient to habitat alteration did not occur in these environments (e.g. *Leptodactylus labyrinthicus*, Heyer, 2005), which indicates that the new environmental filters, arisen as a consequence of replacing native vegetation with rice fields, are more detrimental on Neotropical anurans than expected.

Anuran biomass, phylogenetic diversity, functional diversity, and specific trait diversity were positively influenced by the presence and abundance of landscape features such as waterbodies and forest patches. These metrics increased with decreasing distance to the closest waterbody and increasing waterbody abundance and forest patch area. Hence, these landscape features are crucial for maintaining more diverse anuran communities in agricultural landscapes.

The lower body condition observed in frogs from cultivated sites is an indication that these animals have reduced fitness and suggests that ecologically relevant parameters such as reproductive output and survival may be impaired in these populations (Brodeur et al., 2011).

Meta-population theory, the source-sink concept and adaptations of island biogeography theory all stress that habitat patches vary in their capacity to maintain populations (due to variation in their size, resources, microclimate, etc.), and that a subset of patches may be pivotal to network viability (Whittaker and Fernández-Palacios, 2007). Indeed, meta-population persistence in fragmented landscapes depends on the ability of habitat patches to support resilient local populations and sufficient connectivity between patches. Amphibians are frequently characterized as having limited dispersal abilities, strong site fidelity and spatially distant breeding habitat. Investigating how landscape structure influences amphibian populations is crucial, and measuring connectivity has been recognized as critical to the study of fragmented populations. We found that forest patch area and abundance, as well as waterbody area, were the most important predictors of waterbody importance for connectivity. Although our approach of network analysis followed the simplest model, and cannot be generalized to other cases without caution, our results suggest that in order to maximize pond network connectivity for amphibians in rice crops we must ensure that abundant and large forest patches are present in the vicinities of the breeding sites, and that a network of abundant waterbodies must be preserved or even created.

Anuran communities in crops have considerable economic potential, acting as pest control and contributing to increased crop yield. We believe the patterns we detected on anuran communities are of the utmost importance for managing agro-ecosystems, especially in the Neotropics, where agricultural expansion is unrelenting and biodiversity especially high and unique.

Local diversity, a proportion of regional richness (e.g. Holt et al., 2002; Meatyard, 2005), can be expected to be lower in agroecosystems than in natural ecosystems, because of their high disturbance levels. In fact, crop fields have been described as “defaunated islands, relying on colonization from the regional species pool” (Tscharntke et al., 2005). Managing such disturbed ecosystems depends on a diversity of source populations in the surrounding landscape, which assure the resilience of the systems for sustainable use (Folke et al., 1996).

Although organic farming has been often touted as the solution for ensuring biodiversity preservation in crops, landscape context is also important (Bengtsson et al., 2005). In fact, the species pool of the landscape from which local communities are drawn may be

even more important than the difference between organic and conventional agriculture, For example, Schmidt and Tscharntke (2005) and Schmidt et al. (2005) found the diversity of spiders to increase with landscape complexity, but not farming system. The negative impact of intensive farming may happen only in simple landscapes, with little colonization from the surrounding areas, whereas complex landscapes appear to mitigate the effects of actions associated to the management of intensively grown crops. Hence, in simple agricultural landscapes, such as vast rice crop areas, local habitat creation or management changes may be important for reducing isolation from sources of colonizers, thereby improving ecosystem services (see Bengtsson et al., 2003).

7.4. Management guidelines and implications

Brazil is currently facing extremely high economic demands, which reinforces the need for thorough, viable and cost-effective conservation and management actions.

I recommend the protected areas' network of the Cerrado to be revised to include pristine regions still remaining in the center of the biome, as this is the region with the largest concentration of high extinction anurans, major conservation gaps and strongest anthropogenic pressure. In simple landscapes, such as vast monocultures, local habitat creation or management may be the solution to reducing isolation from sources of colonizers and improve ecosystem services. In concrete, maintaining or creating a network of abundant waterbodies and large forest patches is crucial for sustaining more functionally and phylogenetically diverse anuran communities in these anthropogenic landscapes. Furthermore, earthen irrigation channels and shallow depressions that support perennial ponds and aquatic vegetation are other important features for promoting the use of rice fields by anurans.

7.5. Future research

Given the current economic pressure to converting the Cerrado into a massive agricultural area, the scientific community must make a definite effort to try to preserve what is still left from the world's largest and most diverse savanna. This effort should involve developing more conservation plans, improving the protected areas network and respective

management. However, this is highly dependent on acquiring more knowledge on the biodiversity of this biome and on the threats that human activities pose. The northernmost portion of the biome has been especially disregarded by scientific projects and is now being targeted for agricultural development.

Beyond studies on natural history, conserving and managing the actual anthropogenic Cerrado will require more studies on the effects that human activities have on the biome's biodiversity. This thesis underscores the importance of adopting more integrative approaches, considering species ecology and landscape metrics to better guide conservation and management policies.

7.6. References

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